THE BIOLOGY
OF
SOUTH-WESTERN AUSTRALIAN
TORTOISES

by

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CONTENTS

Section Page

Section Page

1.0 INTRODUCTION

1.1 PREAMBLE

The Australian environment contains the usual opportunities for ecological diversification and, consequently, many of the endemic faunal groups have shown a wide radiation to fill the available ecological situations. The best known of these groups is the marsupials, but there are numerous equally remarkable, for example, Leptodactylid frogs, Agamid lizards, Elapid snakes, Meliphagid birds and Murid rodents. These radiations have, to a large measure, contributed to the uniqueness of the Australian fauna. A parallel occurs in the plants, for example, in the Myrtaceae and Proteaceae.

Apart from marine species the order Testudines is represented in Australia by a single family, the Chelidae, which is a member of the sub-order Pleurodira. Members of this family also occur in New Guinea and South America - a similar distribution to that of the living marsupials. Australian Chelidae are restricted to fresh water situations and, in the absence of the true terrestrial tortoises of the family Testudinidae, are commonly known as "tortoises" to distinguish them from marine "turtles".

The Australian tortoises also show an interesting radiation and occupy habitats ranging from the moist tropics of Queensland and New Guinea to the extremely arid tropical

and subtropical parts of Western Australia as well as the moist mesothermal south-east and south-west.

One member of this group has been instrumental in creating a large amount of public interest in the conservation of the Australian fauna. Until the last decade or so there had been little public interest in conserving fauna and, consequently, government activity had been only indirect, such as the setting aside of reserves when requested. More recently, in Western Australia, all native terrestrial vertebrates have been declared "protected animals" under the Fauna Act, and, apart from those declared as vermin from time to time, they may only be collected under licence. In addition some rarer forms are completely protected and may not be collected. Also, as far as it has been practicable, reserves containing representative habitats have been set aside.

Much of the work of acquiring reserves was unspectacular and little interest in conservation was aroused until the rediscovery of the swamp tortoise Pseudemydura umbrina and, later, the noisy scrub bird Atrichornis clamosus. Public interest in P. umbrina was stimulated both by the peculiar circumstances of its rediscovery within the metropolitan area of Perth and by an appreciation of its apparent restricted distribution and extreme rarity. As a result of this interest the State Government, aided by a public appeal

for funds, was able to arrange that both crown and private land, on which P. umbrina was known to exist, could be set aside, in 1962, as two reserves.

The authorities charged with the conservation of P. umbrina lacked qualified research staff, and, in the absence of a Wildlife Management Department in the University, enlisted the aid of the Department of Zoology in obtaining basic biological information on P. umbrina and laying down procedures for management.

During the spring of 1963 a group of six honours students, supervised by Dr. A.R. Main, made a study of P. umbrina. Emphasis was placed on feeding habits, growth rates, temperature preference and morphological variation, and available information on the life history was collated. A study of the flora and fauna of the two reserves was also made. Following this study some suggestions were made concerning management (Lucas, 1963). However, considering that this study extended over only six weeks, and that only five P. umbrina were captured in the field, it was extremely incomplete and, really, was useful only in indicating that a successful management program would depend on a good understanding of the causes of the rarity, as well as the broader topics of the natural history and ecology of the species. Following this the present study was undertaken as a thesis topic.

A literature search with the aim of understanding something of the biology of P. umbrina highlighted the absence of any previous studies on the radiation of the Australian Chelidae, from the point of view of morphology, natural history or any other aspect of biology. This emphasised the dependence of successful conservation measures for P. umbrina on

(a) the rapid documentation of the natural history and ecology of P. umbrina

(b) providing a reasonable amount of comparative information on other Australian tortoises, particularly with reference to:

(i) natural history

(ii) those factors likely to contribute to habitat preference and distribution

(iii) the relationships and evolution of the group.

This should lead to an understanding of the present limited range and rarity of P. umbrina as well as indicating the proper precautions necessary for its persistence.

1.2 THE TORTOISES OF SOUTHERN WESTERN AUSTRALIA

The systematics of the Australian Chelidae have not been well documented, largely because of the lack of extensive collecting. No major revision of the group has been published since that of Boulenger (1889). Worrell (1963), who largely followed Boulenger, lists eleven species in four genera as

occurring in Australia. A recent revision by Goode (1967) lists 13 species from Australia and New Guinea, one being restricted to the latter.

Three species occur in the southern two thirds of Western Australia and a synopsis of them is as follows:

Pseudemydura umbrina Siebenrock, 1901, the Western Swamp Tortoise, (Plate 1), is a short-necked tortoise which has been found only in a small area of the Swan Coastal Plain, near Perth. It was first known to science as a single specimen in the Natural History Museum, Vienna. It was acquired in 1839 and labelled simply "Nova Hollandia Jun". No further specimens were collected until 1953 when two tortoises were found near Warbrook, 25 miles north-east of Perth. These were described as a new species, Emydura inspectata, by Glauert (1954), but this was shown to be a synonym of P. umbrina by Williams (1958). P. umbrina is a totally protected animal and may not be taken for any purpose. Since this study was done at the instigation of the fauna authorities special permission was given to collect and keep the tortoises, but not to kill them.

Chelodina oblonga Gray, 1841, the Oblong Tortoise (Plate 2) is a long-necked tortoise found in the sub-humid south-west corner of the state. It does not occur in northern Australia, as stated by Worrell (1963). C. colliei Gray, 1855, is a synonym of C. oblonga.

Chelodina steindachneri Siebenrock, 1914, the Dinner Plate or Plate Shelled Tortoise (Plate 3) is a long-necked tortoise found throughout the arid parts of the north-west of Western Australia. C. millymillyensis Glauert, 1922, is a synonym of C. steindachneri.

1.3 COMMENTARY

The small number of species in southern Western Australia, and indeed in the whole of Australia, is well illustrated by the fact that the total geographical range of the above three species is approximately seven degrees of longitude (114°E to 121°E) and 15 degrees of latitude (20°S to 35°S). A similar climatic area of North America or Eurasia might contain many species of several families.

Nevertheless the three species appear to reflect three widely different adaptive modes. P. umbrina, which inhabits temporary water, is adapted to the dry summer and wet winter of a typical Mediterranean climate, C. oblonga is adapted to permanent water and is apparently unable to tolerate a lengthy drought, and C. steindachneri is adapted to arid areas, which are described as EA'd (arid tropical desert, rainfall deficient in all seasons), and EB'd (arid mesothermal desert, rainfall deficient in all seasons) according to the Thornthwaite (1931) classification.

Most other Australian Chelidae inhabit permanent or semi-permanent water so, despite the paucity of the fauna in southern Western Australia, it appears that the major adaptive peaks of the Australian radiation are accessible to study.

Bearing in mind the points discussed in Section 1.1, this thesis has been orientated as follows:

(a) a documentation of the natural history and ecology of P. umbrina together with available comparative data on the more common local species, C. oblonga and C. steindachneri. Unfortunately an extensive field study of C. steindachneri has been prevented both by the distances involved and the poor state of the roads in north-west Australia. In addition, the time taken to obtain results on P. umbrina has precluded a similar study on the other local species, C. oblonga

(b) a comparative physiological study of C. oblonga and C. steindachneri with the aim of elucidating possible adaptations in the latter to a desert environment. Some comparative date on P. umbrina and other species are included in the hope of explaining their habitat preference and distribution

(c) an evolutionary study of the Australian Chelidae, using mainly osteological and serological data.

2.0 FIELD METHODS

2.1 P. UMBRINA

2.11 Capture in water - winter and spring

During 1964, 65, 66 and the first half of 1967 visits were made to the reserves, usually at weekly intervals, for a full or half day. At times visits were made more or less frequently, depending on the season and other commitments. During the early part of the study some visits were made at night, but these were largely discontinued later due to their lack of success. Some considerable time was also spent searching other localities in an effort to extend the known range of P. umbrina.

Initially, baited funnel traps were set in the water in an effort to capture P. umbrina. Baits used were various types of meat and fish. These were, however, unsuccessful because, unlike other Australian Chelidae, P. umbrina is not a scavenger and will not even take meat or fish in captivity unless very hungry.

The only method of capture which proved successful during the first part of the study was to walk slowly through the swamps, when they contained water, and pick up any tortoise seen. This method was very time consuming since, on the average, it took more than 30 man-hours of searching to locate one tortoise. This was largely due to the difficulty in seeing through the water, which, on the Ellen Brook Reserve, has a yellow-brown suspension, and on

the Twin Swamps Reserve is a dark black-coffee colour. Even under ideal conditions of no wind and bright sunlight it is impossible to see a dark object like P. umbrina below a depth of five or six inches. This prevented searching the majority of most swamps which contained water at a depth greater than this. From the lack of catching success it was concluded that P. umbrina prefers deeper water. On overcast days this method of capture was almost completely unsuccessful.

Individuals could occasionally be located when they came to the surface to breathe. Only a few were located in this manner, so either the interval between breaths is great or the tortoises are aware of the searcher and avoid breathing. In an effort to overcome the latter possibility the searcher could stand still in or at the edge of the water, but when this was attempted very few tortoises were seen, probably because of the small field of view due to the vegetation, and it was found to be more effective to walk slowly through the water.

Another method of capture, developed later, was to feel for the tortoises with the hands in water through which visibility was limited. This "puddling" met with considerable success at the beginning of winter and in the early summer when the swamps are limited to a few pools. During the rest of the winter and spring the swamps are

too deep and extensive and the tortoises in too low a density for this method to succeed. Most success with this technique came at the beginning of summer when the swamps had nearly dried up.

As a result of the natural history learned in 1964 and 1965, and especially with an appreciation that the P. umbrina on the Twin Swamps Reserve move from the swamps onto the sandhills during the summer months, a system of traps was constructed during the summer of 1965-66. It consisted of 830 yards of two inch mesh wire netting completely encircling South East Swamp (see Figure 4) on the Twin Swamps Reserve. The wire netting was 15 inches high and the lower four to six inches was buried in the ground. The remainder was supported with stakes and slanted outwards to prevent tortoises heading for the swamp from climbing over it. Pits 18 inches deep, 12 inches wide and about three feet long were dug at 25 yard intervals along the wire (Plate 14).

This method of trapping proved very successful and a total of 27 P. umbrina were caught during 1966. During the same period 40 P. umbrina were captured by puddling and five were picked up while walking through the swamps.

The cost of catching P. umbrina, in man-hours, is given in the table below which compares the time spent obtaining this total of 72 captured in 1966 with the numbers captured during previous years.

Year	No. P. umbrina caught	Man-hours in field	Man-hours per tortoise
1963	4	400	100.0
1964	11	300	27.3
1965	10	300	30.0
1966	72	300	4.2

In 1963 seven people spent twelve days each in the field and about 400 man-hours were spent searching for P. umbrina. During the six months when water was standing in each of 1964, 65 and 66 the author and associates from the Department of Zoology spent about 300 man-hours searching. In 1963 four P. umbrina were caught by the author and associates and one was caught by another person. In 1964 the author and associates caught 11 tortoises and three were caught by other people. In 1965 ten were caught plus one by another person. The man-hours per tortoise in 1964 and 1965 are consistent with the efforts of people before this study was commenced. In 1958 and 1959, in particular, fauna wardens, museum staff and local naturalists undertook many searches for specimens of P. umbrina, but their capture rates on the reserves appear to have been similar.

The extraordinary increase in catching efficiency in 1966 can be accredited partly to the pit traps but also largely to the unusual season (Section 3.3), since the rainfall pattern was such that the swamps on the Twin Swamps Reserve filled only to about one third of their usual depth. This made capture by puddling much easier. Greater knowledge of the habits of P. umbrina also increased efficiency.

2.12 Location - summer and autumn

The techniques discussed so far are only concerned with the capture of P. umbrina during the winter and spring, when the swamps contain water. During the first two summers and autumns no tortoises were found, despite a large amount of time spent searching likely situations.

In an attempt to discover the micro-habitat of P. umbrina during this time of the year, a tortoise was equipped with a housing containing a one-thousand yard reel of cotton thread, which paid out behind the tortoise as it moved. This method was based on the technique used by Stickel (1950) on Terrapene c. carolina. The tortoise was released on April 16, 1964, in a dry swamp on the Twin Swamps Reserve. Its location was checked at frequent intervals until May 7, when the experiment was terminated.

This method of tracking was successful but its main limitation was that it would not work in water as well as on

land and P. umbrina were only available when the swamps contained water. Also, the housing for the reel of thread was very bulky, since it could not be built behind a dome, like that possessed by Terrapene and an inverted P. umbrina with such a housing had great difficulty in righting itself.

To overcome the inadequancies of cotton-trailing a radio-tracking system was developed. Transmitters were constructed, using the circuit of Tester, Warner and Cochran (1964). After potting they were glued to the tortoise's carapace, together with a quantity of polyurethane foam plastic to neutralise the resulting decrease in buoyancy (Plate 15). Transmitters could only be fitted to adult tortoises since their weight was too great for a juvenile. Tracking was carried out using a converted Fonet 501 Citizens Band walkie-talkie. Details of circuitry and construction methods are given in Appendix One.

The design, construction and tuning of the transmitters was carried out by the author. Considerable difficulties were encountered in the construction of the transmitters because of the amphibious nature of the animal. Previously the circuit had been used only on terrestrial animals and the transmitter normally detunes when placed in water. Problems were also encountered in potting procedures and the affixing of the transmitters to the tortoises.

Radio-tracking was first used in the summer of 1964-65. During November, 1964, five instrumented P. umbrina were released on the Ellen Brook Reserve and two on the Twin Swamps Reserve. Four of the transmitters on the Ellen Brook Reserve functioned well into the summer but those on the Twin Swamps Reserve ceased transmission before the swamps had dried.

Construction techniques were improved in 1965 and tracking was carried out during the winter, two tortoises being followed on each reserve. Due to the low number of P. umbrina captured in 1965, only three instrumented tortoises were released in November and only one of the transmitters functioned well into the summer. Tracking was again carried out during the winter of 1966 and an increased catching success enabled twelve instrumented P. umbrina to be released towards the end of winter. Nine of these were tracked throughout the summer and autumn, and, after a battery change, into the winter of 1967.

After tracking procedures showed that many P. umbrina spend the summer and autumn under fallen branches and leaf litter, some considerable time was spent searching these situations. On one day in particular seven people with rakes searched an area of about 100 yards by 600 yards, but no tortoise was found. This must reflect the low density of the species as well as their ability to conceal themselves most effectively.

2.13 Handling of specimens

All P. umbrina captured were marked for future identification. This was done by filing notches into the marginal scutes and the underlying bone. The right marginals were numbered one to nine starting from the rear, and the left ten to ninety. The three remaining left marginals were numbered 100, 200 and 300. The notches remain clearly visible in adults for more than three years. In the younger juveniles they tend to disappear with growth, but last for at least two or three years in most cases. In very small juveniles the notches were cut with a scalpel, but it is not known how long they will last.

After capture the adults were taken back to the laboratory to have transmitters fitted. Physiological experiments were also carried out on some. Juveniles were often measured, weighed, marked and released immediately after capture, but some were kept for short periods for experimentation. Usually a tortoise was released within two weeks of capture.

Carapace length was measured with vernier calipers from the front edge of the nuchal scute to the rear outer edge of one of the hindermost pair of marginals. The measurement was made in a plane horizontal to the plastron and not around the carapace. A specially constructed pair of calipers was used for the larger species. The width

was measured at the point of greatest width. Body weight in the laboratory was measured with a Mettler K 7 balance, and in the field with a spring balance.

2.2 OTHER SPECIES

Chelodina oblonga is a common tortoise and occurs in permanent swamps, lakes and rivers around Perth. Specimens were captured out of the water at two times of the year, firstly when the females leave the water to nest in October and November, and secondly in May and June, when tortoises which have moved into permanent and often saline water during the summer and autumn, leave it in search of new habitats. This occurs actually while rain is falling. Some C. oblonga were picked up by wading through shallow swamps and some were caught in baited funnel traps.

Chelodina steindachneri was captured chiefly in baited funnel traps. These were made from one or two inch mesh wire netting on a stiff wire frame which measured about four feet long and two feet in diameter. A funnel was made from the netting at one end and the other end was detachable, so the catch could be removed. The bait was wired into the trap so it could not be reached from the outside.

The traps were set in pools in creeks in likely areas. They were placed on a sloping bank with the funnel at the deeper end and part of the upper end out of the water, so that any captured tortoises could breathe. The bait used varied, depending on what was available, but best results were obtained by using galah (Kakatoe roseicapilla). Meat from some other birds and from red kangaroo (Megaleia rufa) was also used with success.

Some C. steindachneri were captured using hand nets and a spotlight at night. This technique is particularly suited to the small steep sided pools which occur in creeks passing through rocky country.

3.0 BIOLOGY AND NATURAL HISTORY

3.1 MORPHOLOGY

3.11 P. umbrina

The externals of P. umbrina have been previously described (Siebenrock 1901, 1907; Glauert, 1954; Williams, 1958). The colour of living specimens varies with the type of swamp. The carapace is similar in colour to the swamp water and varies from a medium yellow-brown in clay swamps to almost black with a maroon tinge in the black-coffee coloured water of the sandy swamps. The plastron is a pale yellow-brown with areas of recent growth along the sutures brown-black. Hatchlings are grey above and bright cream and black below.

P. umbrina is the smallest of the Australian Chelidae and adult males do not exceed a carapace length of 155 mm or a weight of 550 gm. Females are smaller than males. The 17 adult females handled during the study had an average carapace length of 125.6 mm (range 120.0 - 133.3) and a weight of about 325 gm (272 - 408). On the other hand 18 adult males had an average carapace length of 140.5 mm (131.0 - 152.6) and a weight of about 400 gm (327 - 540).

The sex of P. umbrina, greater than 110 mm carapace length, can be readily distinguished. Apart from being smaller, females have a flat plastron and a small tail. Males have a concave plastron and a longer, thicker tail.

The shape of P. umbrina varies with age. Figure 5 shows that hatchlings have a length-width ratio of about 1 : 1.7, but they quickly become more circular until, after three months' growth (carapace length 42 mm), the ratio has changed to about 1 : 1.06. One and a half year old tortoises (84 mm) are also the same shape but hereafter the carapace becomes relatively longer until the adult length-width ratio of about 1 : 1.29 is attained.

A figure showing the relationship between carapace length and body weight is also given (Figure 6). Body weight can vary considerably in one tortoise, depending on the degree of desiccation and the quantity of urine in the urinary bladder and water in the lateral bladders (see below). The body weights plotted in Figure 6 are of fully hydrated tortoises with the lateral bladders empty. Usually the tortoises empty the lateral bladders when they are handled, but any remaining fluid was removed by applying pubic pressure with the thumbs.

It is well known that the pattern of scutes (or shields) on the carapace and plastron of turtles and tortoises may differ from the typical pattern. Of 103 P. umbrina examined, 77 (74.8%) showed some variation from the typical pattern for this species (Table 1). However, of the 77 atypical tortoises, only 16 (15.5% of the total) possessed inserted or extra scutes and two (1.9%) had fewer than the normal

number of scutes. Seventy three (70.9%) had some form of division in the mid-line of the second and third vertebral scutes and five (4.9%) had a partially or totally divided nuchal scute. Adult P. umbrina have a vertebral groove in the mid-line of the carapace, but this does not necessarily cause this splitting since it occurs in hatchlings as well, and they have no groove.

Zangerl and Johnson (1957) examined 2,220 Testudines of 118 species and seven families and found that 951 (43%) exhibited one or more scute variations. Many of these variations were heterotopic sulci or incomplete expression of normal sulci. These were not recorded in the present study since they rarely appear in hatchlings or juveniles and seem to be a result of aging. Thus, P. umbrina appears to have a more variable scute pattern than is the average. However, many other species show high degrees of variability.

Most suggested explanations of the origin and significance of scute aberrations are highly speculative and only Lynn and Ullrich (1950) have presented experimental evidence on the problem. This suggested that humidity factors during critical stages of embryonic development causes the abnormalities. Cagle (1950) also showed that the handling of eggs of Pseudemys scripta caused a marked increase in the proportion of scute variability in the hatchlings. Whatever the cause, most abnormalities present

in adults appear to have no effect on the well-being of the tortoise.

Detailed dissection of the soft parts has not been carried out due to the lack of specimens. However, the one or two specimens available showed that, in common with Chelodina oblonga and C. steindachneri and probably all other Australian Chelidae, P. umbrina possesses a pair of bladders opening laterally into the cloaca in addition to the urinary bladder which opens ventrally (Figure 21). When a tortoise is lifted from the water it usually voids a quantity of fluid from these bladders. Analysis (Section 5.3) has shown it to be the same as the water in which the tortoise had been situated. Lateral bladders occur in other Testudine families, but their function is conjectural. Their use in aquatic respiration has been suggested and this seems to be the most tenable explanation. However, the present study suggests that they may also act as a space for the storage of water, which can be utilised by a tortoise, which is forced to remain out of the water for some time.

The osteology of the shell and skull is described in section 6.2.

3.12 Other Species

Chelodina oblonga is normally a dark grey or black, with brown markings above and a pale grey below. It has been shown to be able to change colour from lighter to darker shades, depending on the background (Woolley, 1957).

It is much larger than P. umbrina, attaining a carapace length of at least 270 mm and a weight in excess of two kilograms. These figures are for females, which, unlike those of P. umbrina, are larger than the males. The largest male handled was only 211 mm long. C. oblonga has a particularly long and thick neck. It is about the same length as the carapace and cannot be effectively withdrawn into the shell.

Sexual differences are also evident and are similar to those occurring in P. umbrina. Males have a much longer, thicker tail and a slightly concave plastron while females have a short tail and a flat plastron.

The shape is oblong. The carapace length-width ratio of adults and juveniles is about 1:1.5 to 1:1.75.

Atypical scute patterns are also common in C. oblonga. In a sample of 19 from Shenton Park, Western Australia, ten (52.6%) had inserted scutes and two (10.5%) had vertebral scutes divided in the mid-line. A common pattern in this species is the possession of six vertebrals instead of the typical five.

Chelodina steindachneri is a bright red-brown above, in keeping with the colour of the water in north-west Australia. The plastron and underparts are a pale yellow-brown. It does not grow as large as C. oblonga and has a relatively shorter, thinner neck, which can be withdrawn into the shell.

Like those of C. oblonga females grow larger than males. The largest female handled during this study had a carapace length of 191 mm, while the largest male was only 161 mm long.

Sexual differences are not so obvious as in the other two species. The sex of C. steindachneri can only be distinguished by applying pubic pressure with the fingers or thumbs. If the tortoise is a male it will then extrude its penis. Females do have a slightly smaller tail but the difference is hard to distinguish.

C. steindachneri are nearly circular in shape. Carapace length-width ratios average 1:1.15.

Atypical scute patterns are also common. In a sample of 33 from Wiluna, Western Australia, ten (30.3%) had an inserted scute and one (3.0%) had a scute less than typical. None had scutes split in the mid-line.

3.2 GEOGRAPHICAL RANGE

3.21 P. umbrina

The known range of P. umbrina is extremely restricted. Almost all specimens have come from the two reserves at Upper Swan and Warbrook, or from land within four or five miles of them. The greatest distance from a reserve that specimens have been obtained is eight miles - at Middle Swan and Swan View (Figure 2). It still occurs on land near the reserves but the absence of summer refuges on cleared land is limiting.

Reports of sightings at Mogumber, 70 miles north of Upper Swan, and Pinjarra, 60 miles south, and Donnybrook, 150 miles south, have been made but these have yet to be confirmed by the collection and positive identification of specimens.

3.22 Other species

C. oblonga occurs only in the south-west corner of Western Australia (Figure 1), wherever there is permanent or semi-permanent fresh water. Reports of this species in northern Australia are incorrect.

C. steindachneri ranges throughout the north-western parts of Western Australia (Figure 1). Collecting has not been thorough but it is thought to occur north to the De Gray River, east to Windich Springs and the Wiluna district and south to the Irwin River.

3.3 CLIMATE

3.31 P. umbrina

The climate of the Upper Swan-W[illegible]brook area is typically Mediterranean, with fairly heavy winter rainfall and a dry, warm to hot summer.

The Swan Viticulture Research Station, which is situated half a mile west of Ellen Brock Reserve and three miles south of Twin Swamps Reserve, is a recording station for the Commonwealth Bureau of Meteorology and has kept weather records for the past ten years. Rainfall at this station is summarised as follows:

SWAN RESEARCH STATION

Monthly rainfall July, 1957 - June, 1967 in Points.
Mean and range (one point = 0.01 inch)

January	30	(2 - 120)	July	745	(198 - 1240)
February	27	(0 - 64)	August	419	(86 - 648)
March	54	(0 - 195)	September	210	(48 - 345)
April	147	(8 - 339)	October	185	(74 - 405)
May	436	(27 - 1005)	November	65	(5 - 231)
June	629	(107 - 1284)	December	57	(5 - 110)

Yearly Rainfall (inches)

1958	21.17	1961	28.86	1964	41.84
1959	16.53	1962	29.77	1965	34.55
1960	26.45	1963	39.46	1966	24.53

The annual average of 28.86 inches is probably lower than the true figure because of the short period of records. The totals for 1958 and 1959 are suspect since Belvoir, three miles to the south, recorded 29.81 and 21.26 inches respectively. The annual average at Belvoir (73 years) is 30.80 inches. Unfortunately, this station ceased recording in 1961.

Ellen Brook Reserve probably receives more rain than Twin Swamps Reserve because it is closer to the Darling Scarp. The Climatic Survey, Region 15 - Metropolitan, Western Australia (Commonwealth Bureau of Meteorology, 1966) shows the Ellen Brook Reserve within an area having an average rainfall of 32 to 34 inches, and the Twin Swamps Reserve within an area having an annual average of 30 to 32 inches.

Most rain falls during the months May to October, with June and July the wettest months. The swamps on the two reserves contain standing water for different times each year, depending on the type of swamp, as well as the rainfall, but water is usually present on the Ellen Brook Reserve from late May, or early June, until mid-November and on the Twin Swamps Reserve from mid-June until mid-December. However, the amount and pattern of rainfall can have a marked effect on the duration of the swamp. In 1964

41.84 inches of rain fell and South East Swamp, on the Twin Swamps Reserve, contained water until the middle of January, 1965. In 1966 rainfall was below average (24.53 inches) and swamps on the Twin Swamps Reserve did not start to fill until mid-July and were dry by the end of October. The duration of standing water on the Ellen Brook Reserve is not affected so much by differing rainfall, because the clay soil holds water better and the swamps fill more easily. However, when they have filled to capacity the surplus water drains away into Ellen Brook and they do not continue to deepen like some swamps on the Twin Swamps Reserve.

The way the rain falls is also important. A given amount of light rain, spread over a long period, will not fill the swamps as much as the same amount of rain falling heavily in a short time and producing more run-off. Normally, much of the rainfall is heavy and falls of two or three inches of rain in 24 hours are not uncommon.

Temperatures during the summer months often rise above 30°C and occasionally rise above 40°C. The highest maximum recorded at the Swan Research Station is 44.5°C. During the winter maximum temperatures are usually between 15° and 20°C and overnight minimums may drop as low as 4°C. Frosts are recorded occasionally.

3.32 Other Species

The climate of the area inhabited by Chelodina oblonga is largely similar to that discussed above. The species is limited to areas which have more than about 25 inches of rainfall per year and in parts of its range the average rainfall is over 40 inches. Temperatures throughout its range are similar to those at Upper Swan, although those on the south coast would be a few degrees colder.

Most of the range of Chelodina steindachneri has an annual average rainfall of less than ten inches and some of it has less than eight. Most of this rain is the result of summer tropical cyclones, so the creeks inhabited by C. steindachneri would only run for a few days per year. Maximum temperatures over 40°C are relatively common and the temperature may rise over 45°C on occasions.

3.4 HABITAT

3.41 P. umbrina

P. umbrina appears to be restricted to temporary swamps where soils are either clay or sand over clay and which have suitable aestivating refuges nearby. These two soil types are typified by the two reserves to which the tortoise is largely restricted at the present time.

Ellen Brook Reserve (Figure 3) is located at Upper Swan and lies to the west of the Great Northern Highway, at the 21 mile peg. It has an area of about 155 acres of which only about one quarter is inhabited by P. umbrina.

The soils of this part are mapped within a gilgai complex and a clay-pan complex by Pym (1955). He describes the gilgai complex as having "a characteristic microrelief of puffs and sink-holes..... The profile at the top of the puff is that of a Bellvue clay loam, whilst the material found in the sinkholes is a dark brown loam or sandy loam over a brown or yellow-brown mottled clay at two inches. Sometimes tunnels lead away from these depressions..... Drainage is poor in the gilgai complex..... The sink holes are miniature swamps while the puff portions are fairly well drained" (p.27).

He describes the clay-pan complex as having "some sink holes. The soil of the elevated portions is sometimes a yellow-brown clay, as described in the gilgai complex, and at others a brown sandy loam over a brown clay at about six inches" (pp. 28, 29).

During the winter and spring the sink holes fill to a depth varying between six and eighteen inches. In the summer and most of autumn they are dry. The tunnels mentioned by Pym (op.cit.) are well developed and occur

in the part mapped as clay-pan complex, as well as in the gilgai complex, although they are less numerous. They are known locally as "crabholes".

The main vegetation of the swamps (Plate 4) is an association of Melaleuca lateritia and the sedges Leptocarpus canus and L. aristatus. Aquatic species include Chara australis, Hydrocotyle lemnoides, Myriophyllum sp. and Pritzelia pygmaea. The puffs are covered by a complex association of annuals and semiannuals, which are dominated by the shrubs Acacia cyanophylla, Viminaria denudata, Melaleuca viminea, Hakea varia and Jacksonia Sternbergiana. The annuals include Drosera gigantea, Neurachne alopecuroides and Verticordia densiflora. The bladderworts Utricularia Hookeri and Polypompholyx multifida are well developed and at least 14 species of Orchidaceae occur. There are scattered specimens of Eucalyptus rudis in the area and large numbers occur along Ellen Brook. A more detailed description of the flora is given by Lindgren (in Lucas, 1963).

Ellen Brook, a tributary of the Swan River, runs through the reserve. It does not flow during summer but does contain permanent pools. These are not used by P. umbrina but are inhabited by Chelodina oblonga.

Twin Swamps Reserve (Figure 4) is located at Warbrook and is three miles north of Ellen Brook Reserve. It is bounded on the north by Warbrook Road and on the west by the Midland Railway. It had an area of 350 acres but has recently been enlarged to about 388 acres.

The soils have been mapped within the Beermullah Association by Bettanay et al (1960), who describe it as consisting of "a pattern of sandy and solonetzic soils ..... The soils are of low agricultural value, being poorly drained and high in soluble salts owing to the presence of an impervious pan at shallow depths" (p.9).

On the reserve low, stable sandhills surround the swamps in the eastern and southern parts and the north-western part is uniformly low lying. The swamps and low lying areas have a sandy surface soil and the impervious white claypan occurs at a depth varying from six to eighteen inches.

The swamps are dominated by shrubs and trees of the genus Melaleuca, the species varying with the type of swamp. In shallow, sandy swamps, which contain a maximum of eight to ten inches of water, e.g. North West Swamp (Plate 6), M. viminea is dominant and clumps of the sedges Leptocarpus canus and L. aristatus abound. Aquatics, such as Villarsia capitata and Triglochin acuta, and clumps of filamentous Algae occur, but not in great density.

In deeper swamps, which may contain up to 24 or 30 inches of water, the dominant species are M. teretifolia and M. raphiophylla. The shallower portions, e.g. the western two thirds of East Swamp (Plate 7) M. teretifolia is more common and clumps of sedges and reeds (Schoenus spp.) occur. Near the edges M. viminea also occurs, together with Calothamnus lateralis. Aquatics are similar to the shallow swamps. In deeper, muddy portions, e.g. South East Swamp (Plate 8), M. raphiophylla is dominant and stands of the reeds Eleocharis acuta and Typha angustifolia occur. The aquatic Ruppia maritima can be very dense and the duckweed Spirodela oligorrhiza is common late in the season.

The sandhills (Plate 9) rise to about ten feet above the swamps. They are covered by a Banksia woodland, the main species being B. Menziesii, B. attenuata and B. ilicifolia. B. littoralis occurs in the parts adjoining swamps. Eucalyptus calophylla, E. Todtiana, Nuytsia floribunda and Casuarina Fraseriana occur in low density, scattered through the woodland and Melaleuca paryiflora occurs in the lower lying areas. The understorey is provided by Jacksonia furcellata, Macrozamia Reidlei and Leptospermum ellipticum and there is a ground cover of such spreading plants as Phlebocarya ciliata, Dasypogon bromelaefolius and Conostylis spp.

The remainder of the reserve is made up of low lying country (Plate 10) which is covered by a plant association dominated by Regelia ciliata. Stirlingia latifolia is also common and may become the dominant species in lower lying areas. Banksia sphaerocarpa, Dasypogon bromelaefolius and Phlebocarya ciliata are also fairly common and the paper bark, Melaleuca parviflora, is scattered through parts of the area. Groves of Acacia cyanophylla occur where the sand is slightly deeper. Annuals include various orchids and the green kangaroo paw, Anigozanthus viridis. Much of the Regelia association is covered by one or two inches of water during winter and early spring.

A more detailed description of the flora, together with a discussion of phytogeographical relationships, is given by Lindgren (in Lucas, 1963).

3.42 Other species

C. oblonga is found in permanent swamps, rivers and lakes, as well as in some semi-permanent swamps, which may be dry for one or two months in some years. Typical permanent swamps and lakes on the Swan Coastal Plain contain three to twenty or more feet of water and have a deep muddy bottom. In the shallower portions reeds, particularly Typha angustifolia and Cladium spp. are well developed and paper barks, Melaleuca spp. and swamp gums (Eucalyptus

rudis) occur. Such a swamp is figured in Plate 11. C. oblonga also occurs in rivers and creeks which flow during the winter and recede to a few pools during the dry months. They may be found in typical temporary swamps in the winter but they move back from these to permanent water when they dry. Near the coast they occur in saline estuaries and have occasionally been reported in the sea near the mouths of rivers or drains. It appears unlikely that they feed in saline waters but they probably use them as a refuge in the hot, dry summer months.

C. stendachneri occurs in creeks and rivers which contain water only in isolated pools for much of the time (Plate 12). These pools may be in rocky or sandy areas but always have a sandy bottom. They are characterised by the River Gum (Eucalyptus camaldulensis). The pools may be dry for several months and occasionally over a year at a time.

3.5 REPRODUCTION

3.51 Pseudemydura umbrina

Reproductive data for this species are necessarily limited since P. umbrina is both rare and fully protected by law. This precludes macroscopic and histological examination of the ovaries and testes.

Burbidge (in Lucas, 1963) found that the sex ratio of P. umbrina was not significantly different from one to one. Figures from the present study confirm this, since, of the 32 adults handled, 16 were of either sex.

Copulation has not been observed in the field. Captive animals copulate at any time during the winter and spring months. Copulation takes place in the water and the male mounts the female from the rear, the concave plastron fitting over the slightly domed carapace of the female. One male, on June 18, 1967, was observed in a similar position in the field. It was apparently attempting to copulate with a female which was fitted with a radio transmitter.

Females lay three to five eggs per annum. A female from the Twin Swamps Reserve, dissected by Dr. W.D.L. Ride (pers.comm.) on September 7, 1959, was found to have five large (circa 20mm diameter) ova in its ovaries. Radiographs were made of seven females captured on the Twin Swamps Reserve during the second half of 1966. Two captured on September 11, and X-rayed on September 15, did not contain shelled eggs. However, of four captured on October 29 and X-rayed on October 31, two contained four eggs, and two five eggs (Plate 13). Another captured on November 18 and radiographed on November 21 also contained five eggs.

Nesting occurs in November or early December. A captive female from the Ellen Brook Reserve laid three eggs on November 23 and 24, 1964, in a trough of water where it was being held temporarily. One of the females which was X-rayed in November, 1966, was placed in a sand filled terrarium. It laid its eggs on December 1, 1966. The eggs were deposited in the soil, the bottom eggs about four inches below the surface and the top egg about three inches below. Nesting has not been observed but it is presumed to be similar to that of C. oblonga which is described below.

Only one nest has been found in the field. Dr. A.R. Main found it on the Ellen Brook Reserve on October 9, 1963. It contained three decomposing eggs. At the time there were two inches of water on the ground above the nest, which was about four inches below the surface of the clay, in the shade of a Melaleuca lateritia and clumps of Leptocarpus canus.

It is interesting to note that the only two clutches from tortoises from the Ellen Brook Reserve contained three eggs compared with four or five from the Twin Swamps Reserve.

The eggs are hard shelled. Three from a female from the Ellen Brook Reserve averaged 34.3 mm by 20.1 mm (33.2 - 34.9 by 19.8 - 20.4) and five from a female from the Twin Swamps Reserve averaged 37.6 mm by 20.0 mm (35.5 - 38.7 by

19.8 - 20.2). The average weight was 8.6 gm. Their shape is symmetrical and not enlarged at one end like a bird's egg. In one egg which was examined the shell was found to be 11.5% of the total weight and eight thousandths of an inch (0.203 mm) thick.

The hatchlings emerge the following May or June, that is about 180 days after laying. No exact hatching date is known in the field but two hatchlings were found on the Twin Swamps Reserve by Fauna Warden S.W. Bowler on May 7, 1964. Dates of emergence in captivity are May 20, 1960, in a terrarium owned by Dr. W.D.L. Ride, and June 6 and July 14, 1966, at the South Perth Zoological Gardens.

3.52 Other Species

Copulating C. oblonga have been observed in captivity and they behave similarly to P. umbrina. It has only been observed in recently captured specimens, during the winter and spring and it is not known whether it takes place at other times of the year in permanent water situations.

The eggs are similar to those of P. umbrina. Thirty-nine eggs from the Shenton Park Swamp averaged 34.9 mm (31.8 - 38.4) by 21.3 mm (19.4 - 23.1). The average weight was 9.3 gm (7.7 - 11.3).

Near Perth nesting occurs in October and November. In 1966 the peak of nesting occurred on October 20. At Shenton Park Swamp females started to leave the water at

1300 hours and nesting continued until midnight. A total of over 40 females nested during this time, and at 1600 hours, 14 were out of the water at once. The air temperature during the afternoon and evening varied from 30°C at 1400 to 24°C at 1630 and 22°C at midnight. There was about eight tenths cloud most of the time and light rain had fallen in the morning. A peak in laying occurred at other swamps near Perth on the same day. Smaller peaks occurred about three weeks previously and on November 11. In 1965 and 1964 most nesting activity also took place during the latter half of October.

The nest is dug at a distance varying from a few yards to half a mile from water. Firm, sandy soil is selected. First a vertical shaft six or seven inches deep and one and a half to two inches wide is dug, using the hind feet alternately. The soil is lifted out on the bottom of the foot which is turned back to form a cup. After the soil is lifted out it is pushed into a heap behind the hole and then the other foot is placed down the shaft and the procedure repeated. When the shaft is finished a spherical chamber with a diameter of about four inches is hollowed out at the bottom. Total digging time is between 15 and 25 minutes.

The eggs are then laid. Eggs appear at intervals varying between 45 seconds and three minutes, the interval becoming greater towards the end of the clutch. Before the eggs are laid one of the hind feet is placed down the shaft and the eggs drop onto it and are pushed to one side of the chamber before the next egg appears. The last two or three eggs may be placed in the shaft if there is insufficient room in the chamber. After laying is complete the shaft is filled in using soil from the heap behind the hole. After a little soil has been pushed into the shaft it is packed down with one of the hind feet. When the shaft is full the tortoise rams down the soil by lifting thd rear part of its body off the ground and letting it fall again. This is continually repeated as it moves around the nest disguising the entrance. The tortoise then returns to the water. The whole procedure takes from 25 to 40 minutes, plus the time spent walking to and from the water.

Various reports suggest that tortoises urinate on the soil either before digging commences or after the eggs are laid. This was not observed. After a nest has been refilled the surface soil often appears damp, but this is because it has been dug from a few inches below the surface.

The eggs hatch the following May or June, that is about 200 to 230 days after laying.

C. oblonga eggs have been successfully hatched in the laboratory. Six eggs which were laid in October 1965 were left in the soil until March 1966. They were then kept in the air at room temperature. Two juveniles emerged on May 22, 1966. The other eggs were either infertile or dehydrated. Thirty eggs from five clutches which were laid on October 20, 1966 were kept in moist peat moss in the laboratory. Six of these hatched between May 7 and May 9, 1967, that is 200 days after being laid. They were kept at a mean temperature of 23°C. The remainder were infertile or died from being too moist.

Some eggs which were laid on October 20, 1966, at Shenton Park, were allowed to incubate naturally. These eggs hatched between May 10 and May 28, 1967, with a peak on about May 24, that is 216 days after laying.

Some hatchlings apparently remain in the nest after hatching, or else hatching is delayed under some conditions, since emerging hatchlings have been seen as late as August. Some hatchlings remain in the nest after hatching, since reports have been received of their being dug up in gardens.

Little data are available on reproduction in C. steindachneri.

The egg number is unknown, but if the eggs are the same size as those of P. umbrina and C. oblonga it is difficult to imagine a female containing more than eight or ten.

Nesting dates and incubation times are also unknown, but available information, based on conversations with residents in north-west Australia, suggests that the eggs are laid in spring (September or October) and hatch in February.

Most of the area where C. steindachneri occurs has summer rain, from tropical cyclones, in late January to March, and it is logical to expect the hatchlings to emerge when the rains come. However, because of the uncertain nature of rainfall in north-west Australia, laying and hatching dates may vary from year to year and from locality to locality.

Some data are available on the incubation times of other Australian Chelidae. Worrell (1963) reports hatching the eggs of Emydura macquaria in ten weeks. Goode (1965) states that E. macquaria nests in November on the Murray River, Victoria, and that a natural incubation took 78 days. Incubation in the laboratory at 29.5°C took 62 to 75 days. Eggs of C. longicollis took a little longer and the eggs of C. expansa, which are laid in autumn and over-winter, took slightly more than a year to hatch. Hausmann (1964)

incubated the eggs of the South American Chelid, Chelus fimbriatus, at 27°C. They hatched in 200 to 208 days.

It can be seen that the eggs of P. umbrina and C. oblonga take considerably longer to incubate than do the eggs of E. macquaria or C. longicollis which are laid under similar conditions, and at a similar time of the year. The advantage of delayed hatching in P. umbrina is clear, since, if the eggs hatched earlier, there would be no water available and the hatchlings would die. Most C. oblonga live in permanent water, but some live in semi-permanent swamps and the long incubation time would be of advantage to these.

The egg number of some other Australian Chelidae is known. Goode (pers.comm.) states that C. longicollis lays from six to 12 eggs per clutch with an average of about ten. C. expansa lays up to 22 per clutch (average about 15) and E. macquaria up to 24 (average about 16).

Thus, it is evident that P. umbrina lays considerably fewer eggs than other Australian Chelidae. This must be chiefly a result of its small size. The eggs are of a similar size to most other species and a greater number could not be contained within the small body.

3.6 GROWTH

3.61 *Pseudemydura umbrina*

Growth rings occur on the scutes of juvenile *P. umbrina*. It is assumed that they occur at intervals of one year because feeding only takes place under water and standing water is present only from June to November or December each year.

Several juveniles have been recaptured at intervals after they were marked and released. However, only one of these showed the predicted amount of growth. It was from the Ellen Brook Reserve. When released on September 9, 1963, it had a carapace length of 98.1 mm and had five rings on its scutes in addition to the birth ring. When it was recaptured on November 11, 1964, it had six rings and was 105.5 mm long. The other recaptures were made on the Twin Swamps Reserve in 1966 and 1967, but these were of no use since little or no growth took place in 1966 due to the unusual season (see below). However, juveniles which were marked in December 1965 and October 1966, and which were recaptured early in the following winter had not grown, confirming that growth does not take place during the period when the swamps are dry. Thus, it can be seen that growth only takes place during the period when standing water is present and the growth ring will be formed at the end of this period.

Cagle (1946) reported a similar yearly growth pattern in Pseudemys scripta elegans, but in this case the formation of the ring is due to the cessation of growth during winter hibernation.

In some other species, however, growth rings do not necessarily form at regular intervals, but may be the result of a temporary change in the physiological condition of the tortoise. Woodbury and Hardy (1948), for example, found that the age of the desert tortoise, Gopherus agassizii, cannot be determined by its rings. This is also the case for Chelodina oblonga and C. steindachneri. The former usually occurs in permanent water and may feed throughout the year, while the latter occurs in temporary water which may be present for varying times each year. Elseya dentata is a species which has marked growth rings which do not disappear in the adults and a study of it might be fruitful.

Since the hatching date of P. umbrina is May or June (Section 3.5) the first growth ring will occur in November or December the same year when the water dries up. Growth then does not recommence until the following winter. In older juveniles the inner rings are absent because the scutes are shed every two or three years and these rings are gradually obliterated. Thus, in a three year old

P. umbrina the ring around the hatching scute is no longer clearly visible, but the first, second and third rings which occurred at six months, one and a half and two and a half years of age, are still visible. Similarly, in a six year old tortoise, only rings number four to seven are still visible. However, by the comparison of tortoises of different sizes a complete picture can be built up. Adults possess none of the juvenile rings, but since they keep growing slowly, apparently until death, narrow rings may be visible near the edges of the scutes.

The width of the first vertebral scute of the carapace has been used as a guide to growth. The width of the scute, and of any rings on it, was measured with vernier calipers, at a point half way between its front and rear edges. When the total width of this scute is plotted against carapace length (Figure 7) it can be seen that the width increases linearly until the tortoise exceeds a length of 100 mm. After this, the carapace length increases at a greater rate than the width of the scute. This is correlated with the change in the length-width ratio (Figure 5). However, the width of the first vertebral scute is fairly constant for a given carapace length.

Data for juvenile P. umbrina captured on the Twin Swamps Reserve are summarised in Table 2. This gives the

probable growth rate of juveniles when the swamps hold water for six months every year. It shows that the tortoises can attain a carapace length of 120 mm and a weight of 250 gm at five and a half years of age. One hundred and twenty millimetres carapace length is the size of the smallest female known to lay eggs. The size of males on attaining sexual maturity is unknown, but a captive male of 131 mm has been observed copulating.

Actually, the amount of growth differs from year to year. Table 3 shows the average size attained by hatchlings by the end of the first growing season, in the years 1963 to 1966. It can be seen that the amount of growth depends upon the period when feeding can take place. This is particularly evident in tortoises which hatched in 1966 when water was present for only three months instead of the usual five to six. They grew to only one third of the weight attained by hatchlings in normal years. In 1966 water was present from mid July to mid October and the fact that the hatchlings grew to one third of the normal weight instead of a half suggests that most growth takes place in late spring and early summer when the water is warmer (see Section 4.2).

The figure of five and a half years to sexual maturity for females is, therefore, probably too low. It would be

unusual to have a number of successive years with average, or above average, rainfall. Also data on near adults are scarce and females may grow more slowly than males when nearing maturity. Thus the average number of years to sexual maturity is more likely to be seven or eight depending largely on the annual rainfall.

Data on growth of P. umbrina from the Ellen Brook Reserve are limited but it appears that the rate of growth is lower there than on the Twin Swamps Reserve. A juvenile captured at the end of the 1966 growing season had a carapace length of 61.0 mm and a weight of 44 gm. It had hatched at the beginning of the 1965 winter and had reached a carapace length of 50 mm and a weight of about 27 gm by the end of 1965, compared with 63 mm and 45 gm attained by hatchlings on the Twin Swamps Reserve. Another juvenile was captured on January 27, 1965. It had probably hatched in 1960 and had a carapace length of 99.5 mm and weighed 150 gm. P. umbrina of a similar age on the Twin Swamps Reserve are about 114 mm and 215 gm.

It would appear, therefore, that the tortoises on the Ellen Brook Reserve take at least two years and possibly three years longer to attain sexual maturity. This must be mainly due to the shorter duration of the growing season since the swamps on this reserve usually contain

standing water for only five months each year instead of the six to six and a half months on the Twin Swamps Reserve (Section 3.3). Food may also have an effect (Section 3.7).

3.62 Other Species

No data are available on the growth rates of Chelodina oblonga or Chelodina steindachneri. At hatching C. oblonga has a carapace length of 29 to 33 mm and weighs 4.4 to 7.1 gm.

3.7 FOOD

3.71 Pseudemydura umbrina

P. umbrina is carnivorous. The stomach of a female (from what is now the Twin Swamps Reserve) which was killed and dissected by Dr. W.D.L. Ride on September 7, 1959, and examined by Dr. D.H.D. Edward (pers.comms.) contained aquatic crustaceans, insects and insect larvae. Inspection of the faeces by Graham (in Lucas, 1963) showed that they also eat small tadpoles.

Inspection of faeces during the present study has largely confirmed the above observations. It is also probable that a significant part of the diet on the Twin Swamps Reserve may be an aquatic earthworm of the genus Rhododrilus. This earthworm is very common in the top two

or three inches of soil in the bottom of the swamps and the tortoises are thought to dig them out leaving characteristic depressions (Plate 7). Unfortunately, the presence of these "feeding depressions" in a swamp does not necessarily mean that P. umbrina occurs in it, because other animals, particularly ducks, also feed on the earthworms. Rhododrilus sp. do not occur in the clay swamps on the Ellen Brook Reserve. Known foods are listed in Table 4.

Food is thought not to be a limiting factor on P. umbrina on the Twin Swamps Reserve. The swamps on this reserve are very rich in invertebrate life and as the water recedes in late spring and early summer the aquatic fauna becomes particularly dense. However, on the Ellen Brook Reserve the aquatic life, although fairly plentiful, is not present in quite the same density, and this, coupled with the absence of earthworms, may in part account for the lower rate of growth of juvenile P. umbrina there. However, the shorter period of standing water is probably the more important factor (Section 3.6).

P. umbrina will only feed under water. It does not appear to be a selective feeder but eats anything that moves and is catchable. In captivity it will not readily take meat or fish and can only be persuaded to eat them when very hungry.

3.72 Other species

The diet of Chelodina oblonga is similar, except that it feeds readily on carrion and will take small birds such as the young of ducks and coots. A certain amount of plant material is also eaten.

C. steindachneri will also take carrion but it probably does not grow large enough to prey on birds. Otherwise its diet is similar to that of C. oblonga.

4.1 MOVEMENT

4.11 P. umbrina

4.111 General

A total of 21 adult P. umbrina were equipped with radio transmitters (Table 5). Fourteen of these were re-equipped after an initial period, or were returned to the laboratory to have the battery replaced to prolong transmitter life.

Seven instrumented P. umbrina were released on the Ellen Brook Reserve and the remaining fourteen on the Twin Swamps Reserve. Instrumented tortoises were always released exactly at the place where they were captured. Of the seven released on the Ellen Brook Reserve, five transmitted signals for a period long enough for useful information to be gained on their location and behaviour. Similarly, of the fourteen released on the Twin Swamps Reserve, useful information was gained from ten. One tortoise died shortly after release and five transmitters failed shortly after their bearers were released and were lost. Tortoises with transmitters on their backs will eventually peel them off when they next shed the carapace scutes. One tortoise (No. 139) which was lost on November 6, 1964, had shed its transmitter when it was recaptured on December 22, 1965. Other tortoises, which were recaptured up to eight months

after release, had not lost their transmitters, nor did any tortoise lose a functioning transmitter in this way. Adult P. umbrina are thought to shed their scutes about every three years.

The failure to equip a higher number of P. umbrina with transmitters was due largely to the lack of catching success. During the study only 34 adults were captured and four of these were released before radio-tracking was contemplated. Only late in 1966 did the number of tortoises captured exceed the number of transmitters available. In this year 20 adults were captured and twelve of them were released after being equipped with transmitters.

Owing to the extreme shyness and rarity of P. umbrina it has only been possible to make limited observations on behaviour in the field. Most of these observations were made on instrumented tortoises. A summary of the movement and behaviour of P. umbrina on the two reserves is as follows:

4.112 Ellen Brook Reserve

On the Ellen Brook Reserve P. umbrina are found in the water during the winter and spring. They are not territorial and wander randomly throughout the whole of the flooded area.

The flooded area on the Ellen Brook Reserve consists of a series of pools of varying size which have a few yards of dry ground in between them. P. umbrina often

cross these ridges to get to the next pool. One tortoise (No 10♂), which was tracked throughout the winter and spring of 1965, was located at successive weekly intervals about 30 to 50 yards, in a straight line, from its previous position.

When the water is too cold for activity (see Section 4.2) they rest on the bottom in the deepest part of the pool, in a depression or under a fallen branch. At other times they wander round feeding. Mark and recapture data support the information gained from radio-tracking, that the tortoises move randomly throughout the flooded area.

Feeding is thought only to occur in daylight since a tortoise must be able to see the food in order to capture it. During winter and most of spring the water temperature during the night is too cold for activity and the tortoises rest on the bottom. In late spring and early summer water temperatures during the night are higher (see 4.2), but the extent of activity is unknown.

When the shallower pools dry up, usually by early November, some tortoises move directly into the crabholes, while others move into the deeper pools. When these, too, are dry, usually by the middle of November, all the remaining P. umbrina move into crabholes. They usually move from one crabhole to another for a while, particularly if it

rains, but, from the end of December until May, they normally remain in the same location. Some tortoises may emerge from their aestivating sites for a short time in mid-summer if it rains. One juvenile was picked up crossing the adjacent Great Northern Highway on January 27, 1965, during a shower of rain. It was crossing towards the reserve from cleared country and may have been leaving a poor aestivating site, since a light summer shower would not have penetrated into any of the larger crabholes and broken the aestivation of tortoises in them.

The pools start to refill usually in late May or early June but the tortoises do not leave their summer refuges and enter the water until it is fairly deep, usually in mid-June. They then remain in the water for the rest of the winter and spring.

4.113 Twin Swamps Reserve

On the Twin Swamps Reserve the annual cycle of behaviour of P. umbrina is largely similar to that on the Ellen Brook Reserve, but is modified by the different type of country.

During the winter, spring and early summer they are found in the water of one of the swamps. They also may move from one swamp to another, but here the distance is up to 600 to 700 yards instead of less than 50. No reason can be advanced to account for such movements. Within a swamp the tortoises wander throughout the flooded area.

Their behaviour with respect to temperature is the same as the tortoises on the Ellen Brook Reserve. One tortoise (No. 21 ♂) left the water for a period during September, 1966, and hid in litter under a shrub (Regelia ciliata), about 25 yards from the boundary of North West Swamp, where it had been previously located. After it had been out of the water for three weeks it moved into West Swamp, about 400 yards away. North West Swamp was shallower than usual in 1966 and this may have stimulated the tortoise to leave the water.

When the shallower swamps dry up, usually at the end of November, the tortoises may migrate into a deeper swamp or they may stay out of the water until the following winter. After all the swamps have dried, usually by the end of December, the remaining tortoises move from them to their summer refuges. Initially they may hide under litter in the Regelia association, but usually they soon move into the Banksia woodland. For the first few weeks they may move frequently from one refuge to another, but from mid-January until May they normally remain in the same place.

The temporary refuges are usually under leaf litter, commonly from Banksia Menziesii leaves or under fallen logs or branches. The permanent aestivating refuge may be similar to the temporary site or it may be a hole in the ground, resulting from a burnt out tree root, or the digging of

another animal. The only P. umbrina tracked during the summer of 1965-66 spent most of the summer in a disused den of a fox (Vulpes vulpes).

Of the nine tortoises tracked during the summer of 1966-67, three aestivated under leaf litter, three in holes in the ground and three under fallen branches.

When it enters a refuge a tortoise digs itself into the soil so that most of the soft parts of the body, that is the limbs and head, are under or immediately in contact with the soil. The carapace remains above the soil. This is thought to be a way of reducing water loss through the skin (see Section 4.22).

When the first heavy rain falls in late April or early May some of the tortoises emerge from their aestivating sites and move to another location. However, most of them do not leave their refuges until enough rain has fallen for the swamps to start filling. The tortoises will not move into a swamp until there are several inches of water in it. This usually occurs in the middle of June but may be delayed until July in some years. The swamps on the Twin SwampsReserve have a sandy bottom and, although there is an impervious pan at a shallow depth, they do not fill as readily as the clay swamps on the Ellen Brook Reserve (see Section 3.31).

Detailed maps of the movements of three tortoises on the Twin Swamps Reserve are given in Figures 8 and 9. Diagrams summarising the location of P. umbrina on the two reserves at different times of the year are given in Figure 11.

4.12 Other species

Little information is available on Chelodina oblonga or C. steindachneri. C. oblonga is found in permanent swamps, lakes and rivers and it does not appear to move from these except to nest. Some C. oblonga live in semi-permanent swamps which may dry for two or three months in late summer and autumn. The tortoises are thought to either move to nearby permanent water or hide up under fallen paper barks (Melaleuca spp.). When the first heavy winter rains fall many C. oblonga are found out of the water, usually while the rain is falling. These tortoises are thought to be searching for new habitats, especially for temporary swamps, where food will be more plentiful. This exodus is particularly noticeable from saline waters, such as the Swan River estuary. Reptiles, which continually live and feed in hypertonic saline water, have been shown to have extra-renal salt excreting glands so that they may maintain normal electrolyte concentrations, since their kidney cannot excrete a hypertonic urine (Schmidt-Nielsen and Fänge, 1958). C. oblonga has no such gland (Section 5.33)

so it probably does not feed in salt water, but merely uses it as a refuge during the summer. It then leaves the salt water with the onset of winter.

Attempts were made to radio-track C. steindachneri in order to find out where it goes when the pools it inhabits are dry. Four C. steindachneri, captured in Poonthoon Pool on Mileura Station, 100 miles west of Meekatharra in November 1965, were equipped with radio transmitters. However, heavy rain fell before they were released and the pool reflooded. A similar situation occurred in 1966 when, although no tortoises were released, preparations were under way. It would be most interesting to find out exactly where this species aestivates. Discussions with residents in north-west Australia suggest that they either bury themselves in the creek bed or beneath litter and reeds on the bank. One C. steindachneri was found buried in a homestead lawn. Another possibility is that they move into burrows dug by Varanus gouldi.

4.2 ENVIRONMENTAL INFLUENCE

4.21 Temperature

4.211 General

It is well known that the body temperature of reptiles is of great importance in the regulation of their activity and metabolism and that many reptiles behaviourally control their body temperature within certain limits when possible. The behavioural regulation of body temperature is particularly well developed in diurnal lizards (Cowles and Bogert, 1944; Norris, 1953; Dawson and Bartholomew, 1956; Licht, Shoemaker, Dawson and Main, 1965).

Freshwater tortoises and turtles have a problem in that their body temperature is limited by their environment much more than terrestrial poikilotherms. Water, particularly deep water, does not change temperature rapidly and the only way for a tortoise to raise its body temperature above that of the water is to leave it and bask in the sun. However, this can only be a temporary respite from low temperature since it must return to the water to feed.

Brattstrom (1965), in a review of reptile body temperatures, reported that Testudines are active over a much wider range of body temperatures than terrestrial lizards and that the mean and range varies with the species and family.

4.212 P. umbrina

In an earlier study, Lucas (1963) placed a number of P. umbrina in a photothermal temperature gradient and monitored their body temperature. The air temperature in the gradient varied from 52° to 20°C. The P. umbrina regulated their body temperature fairly well within a range of 22° to 27°C. However, the temperature at the lower end of the gradient was higher than the water and air temperatures met by P. umbrina for much of the winter and spring months, and some of them remained at the lower end of the gradient for much of the time.

Some Chelodina oblonga were also tested in the gradient but they did not regulate, merely blundering from one end of the gradient to the other. Such behaviour reflects the wholly aquatic nature of this species.

In another series of experiments Leung (in Lucas, 1963) investigated the activity of P. umbrina and C. oblonga in water at various temperatures. He found that P. umbrina was normally active at body temperatures between 14° and 28°C. Below 14° activity became very intermittent, and above 28° activity was directed towards attempts to leave the water. C. oblonga, again, did not react well to the experimental procedure, but its preferred body temperature appeared to be between 16° and 28°C.

During the present study all temperatures were taken with a Schultheis quick-reading mercury thermometer. Body temperatures were taken by inserting the thermometer into the cloaca. Air temperatures were taken in the shade approximately three feet above the ground or water.

Body temperatures of P. umbrina captured in the water largely confirmed the results of Leung (op. cit.). Data are insufficient to be presented except as a generalised description. Much of it is from transmitter-equipped tortoises.

After the swamps fill in late May or June, and during July and August, the water temperature is often below 12°C overnight and during the first few hours of daylight, and rarely rises above 16° to 18°C during the day. P. umbrina with body temperatures below 14° were torpid, lying on the bottom of the swamp and usually hidden below reeds or a fallen branch. Those with body temperatures above 15°C were usually actively swimming and feeding, often in the shallower water, which is a little warmer.

In the spring months of September and October water temperatures are higher in the daytime but still low overnight. In shallow water on a sunny day temperatures in excess of 30°C may occur. Active tortoises handled during these months had body temperatures ranging from

16° to 27.5°C (average approximately 22°C). Inactive P. umbrina had body temperatures ranging from 12° to 16°C. During late spring and early summer (November and December) the water temperature continues to rise as the weather becomes warmer and the water shallower. During the night water temperatures rarely drop below 16° and, in the middle of the day, the temperature varies between 25° in the deeper parts and well over 30° in the shallows. P. umbrina body temperatures were usually between 20° and 28°C. When no water cooler than 28° to 30°C is available, the tortoises leave for their summer refuges. This is usually only one or two days before the water dries up completely.

Although feeding takes place throughout the time when there is standing water, it can be seen that during the first three or four months P. umbrina spend much of the time inactive because of sub-optimum temperatures. However, during the late spring and early summer their body temperature is almost always in the preferred range and usually towards the top of it. It is during this time that almost all the growth occurs. This is particularly evident when comparing the growth of hatchlings in various years (Table 3). In 1966 standing water was present from mid-July to late October (three months) and hatchlings grew from an average

of 5.8 gm to 17.1 gm, a gain of 11.3 gm. In an average year, water is present from mid-June to mid-December (six months) and growth is from 5.8 gm to approximately 50 gm, a gain of 44 gm. Thus, in a normal year, four times as much growth occurs in only twice as much time. This shows the large amount of growth during the warmer months.

Captive P. umbrina often come ashore and bask in the sun during the winter and spring. Only one P. umbrina has been observed basking in the field. This tortoise was an adult male and had climbed from the water onto a clump of Leptocarpus canus in North West Swamp on the Twin Swamps Reserve. It was captured at 1130 hours on August 4, 1966. It had a body temperature of 19.8°C compared with the water which ranged from 16.0° to 17.2° and the air which was 17.0° in the shade and 18.4° in the sun. This P. umbrina moved into the water immediately it became aware of an observer.

Basking appears to be a regular pattern of behaviour in the captive P. umbrina at the South Perth Zoo. It has obvious advantages to a poikilotherm like P. umbrina, whose preferred body temperature is higher than the water temperature during much of the winter and spring. However, the extremely low frequency of observations in the field suggests that it is not so important as might be expected.

During the summer months of December, January and February, maximum air temperatures are frequently above 30° and occasionally above 40°C. Only those P. umbrina which had been equipped with radio transmitters were observed during this time. Initially the body temperature was measured whenever a tortoise was located in a refuge, but it was found that handling caused the tortoises to move to another site and the practice was discontinued. Instead, the temperature of the microhabitat was measured and compared with air and surface temperatures, using two Theiss L. No. 597 Mercury Remote Thermographs, with three recording systems.

The results of recordings made in various situations during the summers of 1965-66 and 1966-67 are given in Table 6. All the recordings were made in situations occupied by transmitter-equipped P. umbrina. Figures given are the mean and range of the daily maximum and minimum temperatures. Readings were made to the nearest 0.5°C. The surface record was made immediately above the tortoise, that is where it was in a tunnel the record was made on the soil, and where it was under litter the record was made on top of the leaves. The probe for recording the air temperature was placed about two feet above the ground and in the shade where practicable. For some records the

air probe was partially in the sun at some time during the day and this, in part, accounts for the high readings. The official air temperatures at the Swan Research Station, which is situated half a mile west of the Ellen Brook Reserve and three miles south of the Twin Swamps Reserve, are given for comparison. Two typical weekly records are given in Figures 11 and 12.

It can be seen that the highest temperature ever recorded in a refuge was 34°C, although air and surface temperatures were frequently over 40°. The critical thermal maximum of P. umbrina (see Section 5.4) is about 42° to 43°C, so the temperature in the refuges is well below the critical point.

In the autumn months of March, April and May, temperatures fall gradually from the summer level, and by May, daily maximum air temperatures are usually below 22°C. Unless there is an early break in the season, P. umbrina remain in their summer refuges during this time and temperature has little effect on their behaviour or well being.

4.213 Other species

Little data are available on the body temperature of Chelodina oblonga. Incidental observations on this species in captivity and in the field suggest that it is active within the range 13° to 28°C. Near Perth C. oblonga is

active all the year round. The temperature of deep, permanent water would not vary as much as the shallow swamps inhabited by P. umbrina and it would be in the preferred range most of the time.

The pools inhabited by C. steindachneri would be much warmer than those further south. Observations on captive tortoises of this species suggest that it is active over the range 16° to 34°C.

Winter hibernation has been reported in Chelidae from Victoria. Goode (pers. comm.) states that Chelodina longicollis, C. expansa and Emydura macquaria hibernate in the mud on the bottom of the water inhabited. Water temperatures during the winter in inland Victoria would be much lower than near Perth, but absolute values are not known.

4.22 Desiccation

When in a refuge P. umbrina dig themselves into the soil so that the limbs and much of the head and neck are just below the surface. Only the carapace is visible when the litter or branch is removed. This behaviour is thought to be a way of reducing water loss through the skin. Some measurements of the relative humidity under leaf litter were made. On hot days the readings were in the vicinity of 50% to 60% (31°C) compared with 25% to 35% (37°C) for air.

P. umbrina desiccates at about the same rate as C. steindachneri (Section 5.2). In a laboratory experiment some C. steindachneri were allowed to desiccate in air at 30°C and 40% relative humidity (Section 5.3). Individuals of a weight comparable to adult P. umbrina lost water at rates between 0.27% per day and 0.32% per day.

The amount of dehydration in some P. umbrina was measured in the field during the summer of 1966-67. These tortoises were equipped with radio transmitters and lost weight as follows:

No.	Dates	Initial Wt. (gm)	% Initial Wt. lost	% per day	Rehydrated Wt. (gm)
57♂	13.10.66 to 10. 2.67	441.8	6.4	0.053	443.1
67♀	28.10.66 to 18. 4.67	339.5	16.4	0.095	291.3
31♂	13.10.66 to 18. 4.67	427.9	5.2	0.028	405.2
33♀	13.10.66 to 18. 4.67	308.6	7.6	0.041	300.2

It can be seen that the rates of desiccation in the field are about five times lower than might be expected from laboratory experiments. Field conditions would not be as harsh as those in the experiment described above, but it would appear that the way in which P. umbrina dig themselves into the soil reduces water loss considerably.

The desiccation rate of No. 67 ♀ is much higher than the other three tortoises, but its weight after rehydration suggests that some of the weight loss is due to the laying of eggs. Five eggs would account for a loss of approximately 43 gm or 12.6% of its original weight.

All the weight losses in the above table are considerably below the lethal level. C. oblonga dies when it has lost 32% of its body weight and C. steindachneri at about 38% (Section 5.2). The figure for P. umbrina is unknown. It may be a little lower than the above species since P. umbrina has a higher proportion of bone in its body, but it is most unlikely that it is below 25%.

The desiccation rates of juveniles would, however, be higher. The normal weight attained by a hatchling at the end of its first growing season is 50 gm and the experiments on the water loss of P. umbrina (Section 5.2) indicate that a 50 gm tortoise has a desiccation rate 2.4 times higher than a 400 gm tortoise. If 6% is taken as the normal summer weight loss of a 400 gm tortoise then a 50 gm one will lose 14.4% of its body weight over the same period. A 17 gm tortoise, which is the size attained by hatchlings in 1966, will lose water at four times the adult rate and will, therefore, lose about 24% of its body weight.

Six per cent loss for the summer is probably a conservative figure and it may be concluded that the 1966 hatchlings had a poor chance of surviving the 1966-67 summer. None were found during 1967.

The desiccation rates of the other species are compared in Section 5.2.

4.3 POPULATION SIZE AND COMPOSITION

4.31 P. umbrina

Data on the numbers of P. umbrina on the two reserves are insufficient to calculate the total population with any accuracy. However, it is clear that they occur in much lower numbers on the Ellen Brook Reserve than on the Twin Swamps Reserve.

Four marked tortoises were released on the Ellen Brook Reserve in 1963. In 1964, nine P. umbrina were captured, of which two were marked. Eight of these were released, one being dead when found. During 1965, two P. umbrina were found, of which one was marked. These were also released and during 1966 three were captured, of which two were marked. By simple proportion this gives population estimates as follows:

1964 - 18
1965 - 20
1966 - 17

These estimates may be very inaccurate because of the low numbers handled and the possibility of biased sampling, but they do suggest that the total numbers are very low.

On the Twin Swamps Reserve, numbers are much higher. In 1963, 1964 and 1965, ten P. umbrina were marked and released. During 1966, 69 tortoises were captured of which four were marked. By simple proportion this gives a population estimate of 173. Up to July 1967, ten P. umbrina were captured, of which four were marked. This gives an estimate of 198. In addition three tortoises bearing radio transmitters fell into the pit traps. If these are considered in the sample, the estimate becomes 147.

Once again the estimates may be inaccurate. The 1966 figure may be lower than the true population size since the sampling of the different swamps was not equally intense. It was impracticable to fence and pit trap all the swamps, and some swamps were more suitable than others for the application of the other capture methods. Some movement by the tortoises between swamps takes place (Section 4.113) but the extent, and hence the mixing of marked and unmarked animals, is not known. Also three of the four recaptures had been fitted with radio transmitters which had ceased functioning. When soaked in water, the glue covering the transmitter is paler than the carapace

and this makes it easier to see the tortoise in the coffee coloured water. The 1967 sample may also be biased since most of the catch came from the pit traps and therefore sampling was not equal in the various swamps.

Another method used to estimate the number of P. umbrina on the Twin Swamps Reserve is as follows. A total of 36 tortoises were caught in South East Swamp during 1966 by pit trapping and puddling and this probably represents the whole population. This swamp is five acres in extent. The total acreage of swamps on the reserve, calculated from air photographs, is 34.4, but only about 30 acres of this is of any depth. Assuming that the number of tortoises per acre of swamp is constant, the total number of tortoises is 216.

The composition of the populations from the two reserves is different, the Ellen Brook Reserve having a lower proportion of juveniles. Of the 13 P. umbrina from that reserve, eight (61.5%) were adults, compared with only 22 out of 79 (26.9%) from the Twin Swamps Reserve. These proportions are significantly different (Chi square = 4.33. One degree of freedom, Yate's correction applied, P 0.05).

4.32 Other Species

Few data are available on the density of other Australian Chelidae and none on population structure or dynamics. Chelodina oblonga can be much denser than P. umbrina. At Shenton Park Swamp, which is about two acres in extent, over 40 females have been observed nesting in one afternoon. C. steindachneri can also be dense. Eighteen were trapped in a pool in a creek near Wiluna. This pool was only 40 feet by 20 feet and eight feet deep in the centre.

4.4 FACTORS AFFECTING PERSISTENCE OF P. UMBRINA

4.41 Factors affecting density

The estimates of the total population of P. umbrina on the Twin Swamps Reserve are in the region of 180 to 200, or about six per acre of swamp. Considering the size of the tortoise, its absence of territoriality and pronounced mobility, and the nature and abundance of its food, one would expect the swamps to support a larger population than, in fact, has been recorded, and it is desired to account for the low density observed and suggest whether it will increase or decrease.

It is known that the annual number of eggs produced is only three to five, the latter being the maximum possible, and that this is much fewer than the number produced by other Australian Chelidae (Section 3.51). Such a low fecundity would not, on its own, result in a low density population, unless the reproductive life is short and recruitment is consistently much less than maximal.

The longevity is not known and hence neither is the total number of eggs a female can produce in her lifetime. However, the estimated time to sexual maturity is long (Section 3.61) and, therefore, it is reasonable to expect a long life span under optimum environmental conditions.

An examination of the proportion of the various age classes may indicate the amount of recruitment from year to year. Since the low rainfall of 1966 caused the death of the hatchlings from that year, an examination of the rainfall may show a correlation of recruitment with rainfall. Sixty nine *P. umbrina* were captured in 1966 and their age classes (calculated from growth rings, see Section 3.61) were as follows:

Year hatched	Number	% of total	Rainfall(inches)
1966	9	13.1	24.53
1965	14	20.3	34.55
1964	19	27.5	41.84
1963	3	4.4	39.46
1962	6	8.7	29.77
1961	0	0.0	28.86
1960	1	1.3	26.45
1959	0	0.0	16.53
Before 1959 (adults)	17	24.7	average approx. 31 inches

A correlation between the number of surviving tortoises and the amount of rainfall in their first winter can be seen. The largest age class is the two-year olds which hatched in 1964, a year of above average rainfall and long swamp life. On the other hand, the rainfall in 1963 was also above average but, in the sample, there are only three tortoises which hatched in this year. It may be that the comparatively dry winter of 1962, and the resulting short duration of standing water in the swamps, either did not allow a usual number of eggs per female or reduced the chance of the eggs hatching. The former reason seems untenable since the dry winter of 1966 had no effect on egg numbers. However, following dry winters, the females lay their eggs well after the swamps have dried and this may, in some way, contribute to the reduced hatching rate. In addition, because of the short feeding season, the quality of the eggs may have suffered. Five eggs, which were laid in captivity, failed to hatch and, although this is only negative evidence, it does not contradict the above suggestion. Furthermore, no hatchlings have been found in the field in 1967, although some were found early in the previous three winters.

The tortoises listed in the table as having hatched in 1962 and 1960 may be somewhat older. During 1966 little

growth was recorded in one and two-year old tortoises and none in older juveniles. Thus, a tortoise which appears to be, say, four years old, may be older if it has survived one or more years of below average rainfall. This may be so in the present case since the years 1958 to 1962 all had below average rainfall. In any case it can be seen that there is a very low survival rate of the hatchlings from years that were drier than normal. As discussed above, this is probably due to insufficient growth in the first winter and consequent death by desiccation during the following summer. In addition, it would appear that recruitment suffers even if the rainfall is only slightly below average.

However, recruitment can be quite high in good years. Of the estimated population of 200, 25% are adults, and, since the sex ratio is equal, half of these are females. At an average of four eggs each these females would produce about 100 eggs per year. There has probably been little or no recruitment into the adult age class over the past few years due to the 1958-62 drought, so the number of eggs probably would have been no smaller during this time. If anything, the number of eggs may be on the decline due to the death of senile females.

The age classes present in the 1966 sample can now be used to measure the rate of recruitment from year to year. Two-year olds were 27.5% of the sample, which gives a total of 55 on the reserve. This shows that approximately one half of the eggs laid in 1963 hatched and the hatchlings survived until 1966, implying that, under the optimum conditions of a run of two good winters, recruitment can be high. Mortality might be expected to be fairly low after the first summer as long as the second winter allows some growth and fat production, because of the reduced rate of desiccation with increased size. This is borne out by the one-year old age class, which has a calculated size of 41, only a few less than the two-year olds. Hatchlings from 1965, a year of average rainfall, grew less than 1964 ones (see Table 3) and this may explain the greater mortality, but it does indicate that most of the deaths occur as eggs or during the first summer. Thus, recruitment can be fairly high, given suitable weather.

The high proportion of juveniles in the population suggests that it may be recovering from a period of poor recruitment (Alexander, 1958). The above discussion suggests that this could be due entirely to the weather.

An examination of the rainfall data from Belvoir, which is six miles south of the Twin Swamps Reserve and which kept continuous records from 1892 to 1961, and from Swan

Research Station for 1960 to 1966, should give an estimate of the number of years of poor and good recruitment in the past and some indication as to whether the recent decline was due only to low rainfall.

A summary of the past annual rainfall is as follows:

	Inches per year			
	<25	25-30	30-35	>35
1892-1910	2	8	4	5
1911-1929	2	5	6	6
1930-1948	3	7	5	4
1949-1966	4	6	5	3
Total	11	26	20	18

It can be seen that there is a slight trend towards more very dry years and fewer very wet years. However this would not appear to be great enough to be very significant.

If it is assumed that an annual rainfall below 30 inches seriously reduces recruitment and one below 25 inches prevents any at all, while an annual rainfall above 35 inches enhances recruitment, it can be seen that, on the average, one year in every two has low or negligible recruitment, while one year in every four has good recruitment. In addition, a further examination of the rainfall data shows that the recent period of five dry years (from 1958 to 1962) is the longest run of dry years on record. Three four-year runs of below 30 inches of rainfall occurred in 1904 to 1907, 1935 to 1938 and 1948 to 1951. Thus the recent decline

in numbers is probably largely due to the weather.

Another possible reason for the decline is that the reserves were only set aside in 1962. Previously, the land had been grazed by sheep and cattle and parts had been cut over for firewood. These activities would have reduced the amount of leaf litter and shade, and further increased the chances of death of juveniles during their first summer. This may explain the very low number of hatchlings from years such as 1962, when the rainfall, although below average, was not as low as 1966. These activities would, therefore, have magnified the decline in numbers caused by low rainfall.

Two other factors could affect the density of P. umbrina on the Twin Swamps Reserve. The first of these is predation. The introduced fox (Vulpes vulpes) and possibly feral dogs (Canis familiaris) prey on the aestivating tortoises. One adult female, which was equipped with a radio transmitter, was eaten during March, 1967. It had been aestivating beneath a fallen branch from a Melaleuca parviflora.
P. umbrina has some defence against predators. The carapace and plastron are thicker and stronger than those of Chelodina of the same size and, as in all Pleurodires, the plastron is firmly welded to the carapace by the pelvic girdle, as well as by the bridge. When molested, P. umbrina produce

a strong scent, unpleasant to the human nose, from four glands located either side of the bridges at the junction of the carapace and plastron. However, these defences are evidently insufficient to deter a hungry fox or dog, which can break back the front of the plastron in order to eat the tortoise.

Foxes and bandicoots (Isoodon obesulus) are known to dig up and eat the eggs of Chelodina oblonga and, therefore, probably destroy a proportion of P. umbrina eggs. Birds also may prey on the hatchlings. No evidence of this is available but large wading birds such as the Straw-necked Ibis (Threskiornis spinicollis) and White-faced Heron (Notophoyx novae-hollandiae) feed in the swamps.

It is difficult to assess the magnitude of predation. Some must have occurred in the past, particularly by the now locally extinct carnivorous marsupials Thylacinus cynoceplalus and Sarcophilus harrisi, and more recently by the dingo (Canis familiaris dingo) so, unless foxes are more common now than were other predators in the past, they cannot be blamed for the decline in numbers of P. umbrina. It is reasonable to expect predators to take a proportion of the adults, juveniles and eggs every year. This proportion should, however, be relatively constant from year to year and it is evident that predators do not significantly affect recruitment in years when weather conditions are

optimal. Thus, predation is probably not a significant factor as long as the weather allows sufficient recruitment and the aestivating refuges are maintained.

The other factor which could affect population density is fire. A summer wildfire on the Twin Swamps Reserve would kill a large proportion of the aestivating tortoises. The minority which aestivate in underground refuges (Section 4.113) would probably survive a fire but the removal of the ground cover and canopy would cause higher temperatures in these refuges thus increasing the rate of desiccation, as well as magnifying the chance of death by raising the body temperature above the lethal point. Main (pers. comm.) found that the temperature four inches below the ground at the Ellen Brook Reserve, in the summer of 1962, was 5°C higher where the canopy and ground cover had been recently burned, than where it was unburned. In addition there would be few refuges for any tortoises which survive until the following summer. A fire burned parts of the Twin Swamps Reserve in early 1960, but it was restricted to parts of the Regelia association and some of the swamps, and did not burn any of the Banksia woodland where the tortoises aestivate. No fire has been recorded there during this study.

The Ellen Brook population is much smaller than that of the Twin Swamps Reserve and the proportion of juveniles is significantly lower (Section 4.31). The difference in

numbers is partly due to the smaller area of swamp available, since Ellen Brook Reserve has only 14 acres of swamp compared with 34 on the Twin Swamps Reserve. However, the estimate of the population on the Ellen Brook Reserve is only 20, or 1.5 per acre of swamp.

The low proportion of juveniles suggests that the population is not recruiting as effectively as the Twin Swamps one. This could be due to:

(I) a lower number of eggs per female
(II) a decreased hatching rate
(III) a higher rate of juvenile mortality.

The number of eggs laid by females on this reserve may be only three instead of four or five (Section 3.51). In addition, the nest must be made in clay instead of sand and this may affect the chance of hatching. It may be significant that the only nest found contained decomposing eggs. A higher rate of juvenile mortality is also probable since the growth rate is lower (Section 3.61) and the hatchlings are smaller when forced to aestivate for the first time. Therefore they would be more likely to die from desiccation (Section 4.22).

On the other hand, predation and fire would have little effect. Aestivation takes place in narrow clay tunnels and the tortoises would be protected from predators. The tunnels would also protect them from fire, although frequent fires

might be harmful if they killed the shrubs, the roots of which help support the crabholes. Fire occurred on the Ellen Brook Reserve in early 1960 and 1962, and P. umbrina have survived these. While the fires evidently caused higher temperatures in the crabholes, due to the removal of shade, it is not known if they had any immediate or long term effect on density.

The factors affecting P. umbrina on the two reserves can be summarised as follows:

Factor	Ellen Brook Reserve	Twin Swamps Reserve
Winter and Spring		
Nature of swamps	shallow, clay bottom	deeper, sand over clay
Food supply	poor	rich
Filling of swamps	early	late
Drying of swamps	early	late
Time for feeding	5 to 5½ months	6 to 6½ months
Rate of growth	slower	faster
Time to sexual maturity	9 to 10 years	7 to 8 years
Effect of low rainfall	slight	marked, little growth and reduced survival of hatchlings
Summer and Autumn		
Nature of refuge	clay tunnel (crabhole)	Under leaf litter or fallen branches, in holes in ground
Effect of fire	little	Marked, would kill most of the tortoises
Effect of predators	none	some predation
Effect of plant succession	little, prevention of erosion principal requirement	marked, ideal is climax with maximum ground cover.

4.42 Factors affecting range

The chief factor affecting the range of P. umbrina is the distribution of suitable habitat. The same factors which affect density then control whether P. umbrina can utilise this habitat.

The distribution of suitable habitat is limited. As far as is known P. umbrina only occurs in temporary swamps on a clay or sand-over-clay soil. These kinds of swamps occur in a narrow strip near to and parallel with the Darling Scarp and extend westward along the river courses. In addition, they occur on the Dandaragan Plateau to the north and in sand plain country to the south and south-east of the plain. At first sight, therefore, suitable swamps occur from Dongara in the north to Busselton and Donnybrook in the south, a distance of 350 miles. However, to be suitable for P. umbrina a swamp must fill other criteria:

(I) it must have suitable aestivating refuges associated with it

(II) it must contain standing water for long enough for sufficient growth of hatchlings to take place

(III) it must contain sufficient quantities of suitable food.

Clay swamps are more common than sand-over-clay swamps but gilgai country is not widespread and clay soils do not have a well developed woodland to produce leaf litter.

Climate is also important. To the north of the known range of P. umbrina the annual rainfall becomes progressively lower and evaporation higher, so, unless a swamp received considerable run-off from surrounding country, standing water would not be present for long enough. To the south, where standing water would be present for longer, lower temperatures may prevent normal growth and metabolism.

No data are available on the amount of food in other swamps.

A large amount of possible habitat has been destroyed since the area was first settled by Europeans in 1829. The clays of the Swan Valley are particularly suitable for viticulture and pasture and the Ellen Brook Reserve only escaped drainage because it was set aside for quarrying for clay brick manufacture. Elsewhere on the coastal plain development has also been rapid and few areas of temporary swamps remain in their natural state.

Many permanent lakes and swamps occur on the Coastal Plain, to the west of the strip of clay country, but P. umbrina has not been found in them. It appears to shun permanent water, since, on the Ellen Brook Reserve, permanent pools remain in Ellen Brook during the summer, but the tortoises do not use them.

Due to their great mobility P. umbrina, at some time, must have wandered into permanent water, but apparently they have not persisted there. A possible reason is that the species must undergo aestivation for its physiological well being. However, a captive population of twelve P. umbrina has been held by Dr. W.D.L. Ride and later by the South Perth Zoo, since 1959. Captive tortoises leave the water to bask or simply rest in the shade for a considerable period of time on most days and this may, in some way, substitute for aestivation. Also, apart from the first year of captivity and 1966, this group did not reproduce, nor did the juveniles grow. In 1966 four hatchlings emerged and some slight growth of juveniles was recorded. This may have been due to the introduction of fish for food as well as mammalian meat. Three of the hatchlings subsequently died and the fourth has shown very little growth up to mid 1967, but these conditions can be attributed to the poor quality of the food rather than the permanent water.

Due to its shyness and secretive nature the presence of P. umbrina elsewhere might have been overlooked and it may yet be found in similar country to the north and south of the reserves.

4.43 Synthesis

It has been shown that P. umbrina undergoes a marked seasonal movement, so that they are in the water during the winter and spring and in refuges during the summer and autumn.

The biology of P. umbrina has been interpreted as indicating that optimum conditions for survival and persistence are long, mild winters with heavy rainfall and mild summers, coupled with a suitable habitat of temporary swamps and summer refuges. The summers may be harsh so long as there is adequate shelter for the tortoises, so that their body temperature does not rise above the tolerable range and they do not desiccate too much.

This interpretation lays heavy emphasis on the importance of weather as the factor most likely to affect the chance of P. umbrina persisting. Doubtless a long sequence of dry winters, like that of 1966, followed by long hot summers, would see the extinction of the species.

In the desire to conserve the species it is not possible to regulate the weather, but it is possible to ensure that the tortoises are given optimum conditions to obtain maximum benefit from rainfall by seeing that:

(I) runoff into the swamps is adequate

(II) no drainage that will reduce the depth or duration of the swamps is undertaken.

In addition, the effect of the hot dry summer months can be minimised by ensuring that the summer refuges remain adequate. The latter point is difficult because land-holders and fire control authorities often believe that a climax vegetation with deep litter is a fire hazard to surrounding land, and desire natural bushland to be control-burnt at frequent intervals.

This highlights the fact that management must be of two types, which can be summarised as follows:

Activity necessary for persistence of *P. umbrina*	Activity necessary for public relations
1. Maintenance of habitat by (a) preventing drainage (b) preventing wildfires 2. Controlling predators.	1. Prevention of fire hazard 2. Control of vermin and weeds.

Preventing drainage should not be difficult. The boundary of the Twin Swamps Reserve has recently been extended to include the whole of East Swamp, thus preventing any possibility of the drainage of the swamp from adjoining property.

The danger of an uncontrolled fire on the Twin Swamps Reserve is greater than on the Ellen Brook Reserve and the results would be more detrimental. At the present the reserve is protected by a firebreak ploughed around the perimeter, but a fire jumping this or starting inside it could burn out the whole area. This could be prevented by

making fire breaks within the reserve, so that it is split up into a number of plots, thus restricting any fire to a small area.

The conflict between habitat maintenance and fire hazard can now be overcome by carrying out controlled burning of these small plots in rotation, so that each plot is burned at intervals of a few years. This should be done in spring when the tortoises are in the swamps, and when the vegetation will have dried sufficiently for a fire to run. The interval between successive burns in one area should be worked out using observations on plant regeneration and litter buildup. The firebreaks within the reserve should be designed so that they subdivide the three main types of vegetation, particularly each of the sandhills, thus preventing the destruction of all the refuges in one vicinity.

Ellen Brook Reserve does not constitute a fire hazard because of the low density vegetation and control burning should be unnecessary.

Predator control should be limited to exotic species such as foxes and feral dogs. Rabbits (Oryctolagus cuniculus) also occur on the reserves and should be controlled to prevent damage to surrounding pasture. Weeds are a further problem, especially the exotic Cape Tulips, Homeria collina and H. miniata, which will need to be controlled to avoid reinfestation of surrounding pasture, when this has been freed of them.

It is necessary to follow the effect of these procedures on the tortoises. This can best be done on the Twin Swamps Reserve by continuing the pit-trapping of tortoises entering South East Swamp. As well as giving an annual estimate of population size and past recruitment, such a study should eventually reveal other important information, especially the life span of the adults. On Ellen Brook Reserve numbers are much lower and no simple trapping method is available. Organised searching and puddling, particularly shortly before the swamps dry up, would be the best way of capturing an annual sample.

If the above management procedures are carried out and given suitable weather conditions, the population of P. umbrina on the Twin Swamps Reserve should continue to increase in numbers over the next few years and thereafter persist indefinitely.

The future of the Ellen Brook population is less certain. The numbers there are very low and, since the lowest density from which a population cannot recover is never known until it is too late, it is difficult to predict what will happen. If the population does not increase in the future it may become necessary to repopulate the reserve with tortoises from the Twin Swamps Reserve, but this is undesirable because of the differences in colour and behaviour between the two populations. However, any tortoises found on clay country outside the reserve could be released within it.

5.0 THE COMPARATIVE PHYSIOLOGY OF CHELODINA OBLONGA AND C. STEINDACHNERI

5.1 INTRODUCTION

The Australian Chelidae are wholly aquatic in that they will only feed under water and most species do not leave the water except for nesting or in search of a new habitat when their present one becomes unsuitable.

One would expect, therefore, that the various species would be distributed only in the coastal areas of Australia which have fairly high rainfall. However, the range of *Chelodina steindachneri* in particular (Figure 1) is almost entirely within an area classified as desert, with rainfall deficient in all seasons, according to Thornthwaite (1931), and which, since it has a moisture index below -40 (Thornthwaite, 1948), is designated an arid zone by UNESCO (Meigs, 1954). In addition, *Pseudemydura umbrina*, although it inhabits an area of fairly high rainfall, shuns permanent water and habitually spends six months of every year out of the water.

It would appear, therefore, that the distribution of the Australian Chelidae might, at least partly, depend on the ability of the various species to cope with arid conditions.

This section, therefore, has been designed to investigate some of the mechanisms which may have contributed to the success of *C. steindachneri* in a desert environment.

In order to better understand these mechanisms C. steindachneri has been compared with C. oblonga which inhabits permanent or semi-permanent water in the higher rainfall area of the south-west corner of Australia (Figure 1). Data on P. umbrina have only been obtained where the experimentation could not result in the death of the tortoise, since it is fully protected by law. Data on other Australian Chelidae are included where available.

There are two main problems for an aquatic reptile such as C. steindachneri in a desert environment:

(a) Inadequate water supply. C. steindachneri inhabits creeks and rivers which flow only after sporadic heavy rain. Most of the time the only available standing water is in isolated pools and these may be dry for months, or, in periods of drought, even over a year at a time. There are four ways in which C. steindachneri could overcome a lack of water:

(I) by behaviourally avoiding a desiccating environment

(II) by physiologically controlling water loss through the skin and via the lungs

(III) by storing water which can be utilised as the body fluids are lost by desiccation.

(IV) by tolerating a high degree of dehydration.

(b) High temperature. The summer shade temperature in the area occupied by C. steindachneri is commonly above 40° and occasionally above 45°C. Once the water inhabited by C. steindachneri dries up it comes in contact with this problem. It could overcome it in two ways:

(I) by behaviourally avoiding places of high temperature

(II) by tolerating an elevated body temperature.

It is not known where C. steindachneri goes when the pools which it inhabits dry (Section 4.12) but they are thought to bury themselves in the ground. All the above possibilities, which can be tested in the laboratory, are explored in the following sections.

5.2 DESICCATION

5.21 Methods

Comparative Desiccation Rates

Before being tested the tortoises were kept in clean tap water for at least two weeks and fed with minced meat at weekly intervals. Water temperatures varied between 14° and 24°C.

The tortoises were placed in an oven which was maintained at a temperature of 34± 0.5°C. The air was kept completely dry by placing a tray of drying agent (silica gel) in the oven and circulating the air with a small fan. The loss of

weight of the tortoise was measured over 24 hours. This weight loss was assumed to be due entirely to water loss. If any faeces or urine were passed during a run, the figures were discarded.

Basal Water Loss

A number of tortoises were left in the oven for up to five days until the rate of water loss became constant.

Lethal Dehydration

Some tortoises were allowed to desiccate until they died. The amount of body weight and the proportion of the total body water lost was then calculated. Total body water was found by desiccating the body in an oven at 105°C until constant weight was obtained. Miller (1942) criticised the accuracy of this method but Bradshaw (1965) showed that the distillation of lizards which had been dried in a 105° oven, failed to extract extra water from the tissues.

Respiratory and Cutaneous Loss

Respiratory water loss was measured by placing the tortoise in a plastic bag which was sealed tightly around the neck just behind the skull. It was necessary to tape the limbs into the shell, otherwise the tortoise struggled continuously. The tortoise was then placed in an oven as above. Cutaneous water loss was calculated by subtracting the respiratory loss from the total loss, which was measured separately. Attempts to design an apparatus where respiratory

and cutaneous water loss could be measured simultaneously failed, due to the continual struggling of the tortoises when restricted in any way which did not allow the head to be retracted.

Heart Rate

Heart rates were measured on a standard medical electrocardiogram. The two electrodes were pins placed through small holes bored in the carapace on either side of the heart. The rate was counted with the aid of a stopwatch. The tortoises were placed in an oven at 20°C, in which a tray of water was placed in order to maintain a high humidity and prevent desiccation of the tortoise and the body temperature was monitored by a thermistor taped into the cloaca. Each animal was allowed to settle down for at least a day, until the heart rate was basal. The heart rate was then measured while the body temperature was raised gradually (about 2°C per hour) until it was 35°C. Every effort was made to measure basal rates and, if the tortoise became active, it was allowed to settle down again before heating was recommenced. The body temperature was maintained at 35°C and the heart rate measured at intervals for a further three or four days.

Oxygen Consumption

Initially oxygen consumption was measured in an open circuit system in which air was passed over the tortoise at a known rate and the change in the partial pressure of oxygen determined with a Beckman paramagnetic oxygen analyser. The tortoise was maintained at a body temperature of 35°C and the consumption rates were measured over periods of 20 minutes. It was found that the rates worked out by this method were very variable, apparently because of the infrequent breathing of the tortoises their ability to survive anaerobically for long periods.

To overcome this problem carbon dioxide production was measured over two hour periods. Dry, carbon dioxide free air was passed through a chamber containing the tortoise and maintained at 35±0.5°C. After drying, the air was passed through tubes containing "Ascarite" carbon dioxide absorbent.

5.22 Results

The total rates of water loss of Chelodina oblonga, C. steindachneri and Pseudemydera umbrina are graphed against body weight in Figure 22 and are presented as rate per surface area in Table 7. Surface area was calculated using Benedict's (1932) formula: $cm^2 = 10 \text{ bodyweight } (gm)^{2/3}$. Any surface area calculation has disadvantages when applied to tortoises, partly because of the increased amount of

bone in the body, but chiefly because of the unknown proportion of skin to shell. However, because of the wide weight range of the species which were being studied this seemed to be the best way of making the data comparable.

It can be seen that C. steindachneri and P. umbrina have much lower rates of water loss than C. oblonga. In addition the two arid adapted species can further reduce their desiccation rate over a period of about three days, so that it drops to one quarter (C. steindachneri) and one half (P. umbrina) of the rate for the first 24 hours. On the other hand C. oblonga has a basal rate only slightly below its initial rate.

The figures for cutaneous and respiratory water loss (Table 8) show that C. steindachneri reduces its desiccation rate by reducing both fractions, although the cutaneous fraction drops more, from 70% to 66% of the total. The respiratory and cutaneous rates of C. oblonga both drop slightly from the initial rate but the proportion of cutaneous loss remains the same, at 92 to 93% of the total.

The great disparity in the desiccation rates of C. oblonga and C. steindachneri could be due to two main factors, either different structure of the dermis and epidermis, possibly connected with increased keratinization (Maderson, 1964) or differing ability to control blood flow through the dermal vessels.

Histological examination of the skin showed no difference between the two species, suggesting that C. steindachneri has the ability to control cutaneous water loss by control of blood flow or cell permeability. P. umbrina, on the other hand, appears to have reduced its cutaneous water loss by increased keratinization. No histological sections have been prepared but macroscopic examination immediately shows that P. umbrina has a great amount of scalation on the limbs and heavy tubercles on the neck, which Chelodina lack.

The ability of C. steindachneri to further reduce both the respiratory and cutaneous fractions suggested that it may be able to aestivate. To investigate this heart rates and oxygen consumption were measured on both species.

Heart rates of two C. steindachneri and three C. oblonga are shown in Table 10. It can be seen that, in both species, the heart rate is lower in the larger specimens. A similar relationship was noted in Pseudemys spp. by Hutton et al (1960). However, it is clear that C. steindachneri generally have lower heart rates than C. oblonga but both species are equally able to reduce metabolism, although one C. oblonga maintained high rates throughout the experiment.

Oxygen consumption figures, as reported in Section 5.21, were very variable when measured for only 20 minutes. One C. oblonga had rates varying from 0.003 to 0.037 cc O_2/gm/hour. When CO_2 production was measured over longer

periods more repeatable results were obtained (Table 11). Data are insufficient for detailed conclusions to be drawn, but little difference between the species is evident. Both are able to reduce their metabolic rate when left in a warm atmosphere. Benedict (1932) and Hutton et al (1960) found no correlation between oxygen consumption and body weight in turtles or large terrestrial tortoises, so the figures in Table 11 may be directly comparable. In this way Testudines appear to differ from other reptiles, particularly lizards, where such a correlation has been found (Dawson and Bartholomew, 1956).

Thus, it seems that the main difference in the ability of the two species to control cutaneous water loss is not due to differences in metabolic rate, although this may have some effect.

The great difference in the desiccation rates of the arid adapted C. steindachneri and P. umbrina and the wholly aquatic C. oblonga suggests that this factor is of prime importance in the distribution of the Australian Chelidae. Consequently, water loss rates were measured on a number of other species (Table 9).

The species tested fall into two groups, those with rates greater than 70 mg/cm^2/day and those with less than 40 mg/cm^2/day, although Elseya dentata has a rate in between these groups. All the species in the first group are wholly

aquatic. Of the species in the second group C. steindachneri and P. umbrina have already been discussed. Of the other species C. longicollis is wholly aquatic and its comparatively low rate of water loss is difficult to explain. However its basal rate is nearly as high as the initial rate. C. novae-guineae and Emydura kreffti both occur in northern Australia and may be able to withstand the drying of pools during the dry northern winter. C. novae-guineae is able to reduce its water loss well below the initial rate in a similar manner to C. steindachneri. The one specimen handled had a basal rate of 15.5 compared to the initial rate of 28.4 mg/cm^2/day. E. kreffti has not been tested for this.

Two species of Cryptodire Testudines which were available were also tested. Clemmys caspica leprosa (Emydidae) lives in a similar climate to southern Australian species and is capable of withstanding periods when water is absent. Testudo graeca (Testudinidae) is a completely terrestrial herbivore.

It is interesting to note that the basal rate of C. steindachneri is very similar to the rate measured for T. graeca. Thus, the only thing preventing C. steindachneri from being completely terrestrial is its feeding habits. Schmidt-Nielsen and Bentley (1966) measured the water loss rate of the desert tortoise, Gopherus agassizii at 35°C and found it to be 3.8$\pm$ 0.54 mg/cm^2/day, a somewhat lower rate than that found for T. graeca.

The stage of dehydration which is lethal also differs in the two species. Results of experiments are given in Table 12. It can be seen that C. oblonga dies when it has lost approximately 32% of its body weight, which corresponds to 40% of its body water. C. steindachneri, however, does not die until 50% of its body water has evaporated. No correction has been made for weight loss due to metabolism, and the C. steindachneri, because of their low desiccation rate, took very much longer to die than C. oblonga. At a metabolic rate of 0.06 mg CO_2/gm/hour (Table 11) the 145 gm C. steindachneri would have produced 8.4 gm of carbon dioxide in the 40 days it took to die.

The RQ for starving mammals is 0.7 but figures below this have been found in birds. This is due to the production of uric acid instead of urea and, therefore, tortoises also probably have a low RQ. This means that there is no weight loss due to gaseous exchange, and there may even be a weight gain if the RQ is below 0.7. The other component of fat breakdown is water, which will be added to the body water. Nearly as many molecules of water are produced from fat breakdown as molecules of carbon dioxide. If it is assumed that an equal amount is synthesised the above animal will produce approximately 3.4 ml of water. This changes the value of the amount of body water lost at death from 50.6% to 47.6%. However, it is still clear that C. steindachneri

is able to tolerate a greater degree of desiccation and, anyway, this extra water produced by fat breakdown is of survival value in the field.

5.3 WATER CONSERVATION

5.31 Methods

Sixteen Chelodina oblonga and nine C. steindachneri were acclimated in water at 20° to 23°C for at least a month. During this time they were fed weekly on minced meat.

An initial sample of five C. oblonga and four C. steindachneri were killed and a sample of plasma and urine taken from each. Seven C. oblonga and four C. steindachneri were allowed to dehydrate in an atmosphere at 30°C and 40% relative humidity, and four C. oblonga and one C. steindachneri were allowed to dehydrate at 20°C and 60% relative humidity. When these tortoises had lost 25% to 30% of their initial body weight they, too, were killed and urine and plasma samples taken.

Each tortoise was treated as follows. After weighing it was given an injection of Pentobarbitone Sodium (Nembutol) into the body cavity (dose: 60mg/Kg). Immediately it had lost its eye reflex the plastron was removed and 2 or 3 ml of blood were taken from the heart (which was still beating) with a heparinised syringe. The blood was centrifuged at

3,000 rpm for 15 minutes and, after the haematocrit had been read, the plasma was pipetted off and the cells discarded.

All the urine was then removed from the median bladder with a syringe and the volume recorded. Any solids were removed by cutting the bladder open and everting it. Plasma and urine were frozen at -20°C until analysis. The tortoise was then placed in an oven at 105°C and dried to constant weight for the calculation of total body water.

Sodium and potassium were analysed on a Coleman flame photometer (Models 6C and 21). A 10 µl sample of fluid was diluted in 5 ml of distilled water and both sodium and potassium were measured in the same dilution. Ammonia and urea were measured using the microdiffusion method of Conway (1957). Urates were analysed by the method of Feichtmier and Wrenn (1955). After the concentration of urate in the fluid part of the urine had been measured the fluid was removed and the solids were dissolved in 0.4% lithium carbonate for separate analysis. Osmolality was measured on a freezing point depression apparatus.

5.32 Results

The results are presented in Tables 13 to 16. No differences were noted in the concentrations of the components analysed in the urine and plasma of the tortoises dehydrated at 20°C and 30°C and the results are combined.

The first point of interest is that both species can reabsorb water from the urinary bladder into the bloodstream. No urine was passed by the dehydrating tortoises so this is the only explanation for the decrease in the amount of bladder fluid. A similar reabsorption was noted in Chelodina longicollis by Rogers (1966), and in Pseudemys scripta by Dantzler and Schmidt-Nielsen (1966).

The reabsorption of water would appear to be controlled by two factors: permeability control and active solute transport. The urine of hydrated tortoises is very hypo-osmotic to the plasma, while that of the dehydrated tortoises is nearly iso-osmotic (Table 15). Bladder permeability in the frog is under the control of neurohypophysial hormones (Bentley, 1958; Sawyer, 1960) but no effect of pituitary hormones on bladder permeability or active sodium transport can be demonstrated in the isolated turtle bladder (Brodsky and Schilb, 1960). The adrenal cortex would appear to be a more likely site for any controlling hormone.

Active sodium transport has been demonstrated in the turtle bladder by Brodsky and Schilb (1960, 1965) and Klahr and Brickner (1964) and active chloride transport by Brodsky, Schilb and Spafford (1963). This sets up an osmotic gradient which causes water to follow passively.

The presence of a sodium pump in Chelodina oblonga and C. steindachneri is indicated by the very low concentration of sodium in the bladder fluid of dehydrated tortoises when

compared with the plasma, and the associated very high concentrations of potassium. It would appear that the potassium ions have penetrated the bladder to equalise the difference in electric charge between it and the plasma, a situation somewhat analagous to that found when comparing intracellular and extracellular fluids. This is further supported by the differences in the concentration of potassium in the bladder fluid of the two species, C. oblonga having only a half the concentration found in C. steindachneri. This is consistent with the high concentration of ammonia in the bladder fluid of C. oblonga. The cations measured in the urine and plasma of dehydrated tortoises of the two species are as follows:

Species		mEq/litre			
		Na^+	K^+	NH_4^+	Total
C. oblonga	plasma	220.0	4.2	0.0	224.2
	urine	5.5	69.0	117.3	191.8
C. steindachneri	plasma	165.0	2.9	0.0	167.9
	urine	8.6	145.9	2.7	157.2

It can be seen that the concentration of the measured cations in the urine approaches that of the plasma. Since the urine is also nearly iso-osmotic, almost all the water which can be absorbed from the bladder probably had been when the animals were killed.

The second point of interest is the low concentration of sodium in the plasma of dehydrated C. steindachneri compared with the elevated levels in C. oblonga. Rogers (1966) suggested that C. longicollis possesses an orbital salt gland similar in function to those found by Schmidt-Nielsen and Fänge (1958) in marine reptiles. However, her evidence was only indirect and was not supported by experimentation. Intra-peritoneal NaCl and KCl injections have been given to C. oblonga, C. steindachneri and C. longicollis, both as a sudden load, in a manner similar to Schmidt-Neilsen and Fänge (op. cit.), and as small loads spread over a number of days. These did not cause the secretion of tears. Furthermore, tears which appeared in the eyes of dehydrating tortoises were analysed and found to be isotonic with respect to plasma sodium but with slightly elevated potassium levels (Na/K = 8.7, range 3.8 - 15.8). No reason for the high potassium levels can be suggested, but it is known that potassium levels in mammalian saliva increase when the animals are sodium depleted (Bott et al, 1964). The crystals seen around the eye of C. longicollis

by Rogers therefore must have resulted from the evaporation of normal tears. Similar crystals were seen in all the species dehydrated during the present work.

Thus, it seems certain that Chelodina do not excrete sodium extra-renally and since sodium is not found in the urine, some other explanation for the lack of elevated sodium levels in the plasma of C. steindachneri must be found.

Bradshaw (1965) found that part of a field population of the lizard Amphibolurus ornatus lost a considerable amount of body water by desiccation, but did not have elevated plasma sodiums. He showed that this was due to a shift of water from the intracellular to the extracellular compartment so that, despite a body weight loss approaching 50%, there was no decrease in the blood volume.

The haematocrit figures (Table 14) suggest that there has been little or no concentration of the blood in either C. oblonga or C. steindachneri, but due to the variability of the haematocrit in hydrated animals it is probably unreliable as an indicator of haemo-concentration. The osmolality of the plasma of dehydrated C. oblonga and C. steindachneri is similar. However, this does not necessarily disprove the suggestion that C. steindachneri is maintaining its plasma volume at the expense of its intracellular fluid, since metabolic wastes such as urea would force the osmolality of the plasma up. Urea levels in the

plasma of C. steindachneri are higher than C. oblonga (Table 15).

Plasma sodium has also been found to be lower than expected in C. steindachneri which have been loaded with NaCl intra-peritoneally. Such an experiment is not analagous to dehydration and in these cases sodium levels in the bladder fluid become almost isotonic with the plasma. However, the amount of sodium in the bladder cannot account for all of the disparity and it seems possible that sodium is being stored in the tissues or in the bone. Further work is necessary to elucidate this point.

The third point of interest is nitrogen excretion (Table 16). It can be seen that C. oblonga is predominantly ammonio-ureotelic when hydrated but becomes predominantly uricotelic when dehydrated, although significant amounts of ammonia as well as urea are still present. C. steindachneri, on the other hand, excretes little ammonia and changes from being predominantly ureotelic to predominantly uricotelic. Rogers (1966), working on C. longicollis, reported a similar but less dramatic shift in nitrogen excretion to that found in C. oblonga. However, in that experiment the C. longicollis were only dehydrated to 80% of their original weight compared with 72% in the present experiment and this may account for the different proportion of uric acid.

Moyle (1949) analysed the urines of various species of Testudines living in different habitats and found that those living in aquatic and semi-aquatic situations excreted mainly a mixture of ammonia and urea while those inhabiting dry terrestrial situations excreted predominantly uric acid. This highlights the selective advantage of uric acid excretion when water is not readily available, and tortoises of the genus Chelodina are apparently able to switch from excreting soluble and toxic ammonia and urea, to insoluble urates when water becomes scarce. Urates have the advantage of precipitating out in the bladder and are easily stored in such a way that they do not affect osmolality.

It has been suggested that the stimulus for this switch-over is temperature as well as hydration (Needham, 1942; Drilhoun and Marcoux, 1942), but comparison of Chelodina dehydrated at 20°C and 30°C showed that there was no difference in the proportions of the resulting nitrogenous end products. Similarly, Khalil and Haggag (1960) found no evidence that temperature change could bring about a change in the absolute activity of arginase and xanthine oxidase in the liver of Testudo leithii although higher temperatures favoured xanthine oxidase. However, T. leithii, being a terrestrial herbivore, should excrete mainly uric acid at all times. The stimulus appears, therefore, to be entirely the degree of hydration, although how this is manifested is

unknown. Similar changes in the nitrogenous end product due to dehydration have been shown in alligators (Coulson and Hernandez, 1955), frogs (Balinsky, Cragg and Baldwin, 1961) and lungfish (Buchanan and Hartman, 1959).

Khalil and Haggag (1955) analysed successive naturally voided urine samples from T. leithii and found that the proportion of urea and uric acid varied considerably and that the major constituent was sometimes one and sometimes the other. However, Dantzler and Schmidt-Nielsen (1966) showed that this could have been due to varying amounts of solids being voided in each sample, so the phenomenom of a switchover in nitrogenous end products is probably restricted to normally aquatic animals when they are deprived of water.

It seems clear that the solids excreted by the dehydrated tortoises are chiefly urates, not uric acid. As Dantzler and Schmidt-Nielsen (1966) point out, the pK for uric acid is 3.48, so since the pH of the urine from dehydrated tortoises of both species was in the range 6.5 to 7.5, practically all the uric acid must be in the form of urates. Since potassium is the predominant cation in the bladder fluid it seems likely that the urates precipitate out as potassium urate.

Concentrations of urate in the fluid part of the urine vary considerably. C. oblonga had a mean of 1.87 mM/litre

(0.36 - 4.31) and C. steindachneri 2.46 mM/litre (1.03 - 4.95). The solubility of potassium urate is 12.06 mM/litre and of sodium urate 6.76 mM/litre, so it would appear that precipitation is not caused by concentration, but by some other means. Dantzler and Schmidt-Nielsen (op. cit.) report a similar anomaly in the urine of Gopherus agassizii and suggest that solute exchanges across the bladder wall may in some way cause precipitation.

5.4 TEMPERATURE TOLERANCE

5.41 Method

The critical thermal maximum (CTM) was originally defined by Cowles and Bogert (1944) and has been modified by other authors. Hutchison (1961) uses the definition "the value that is the arithmetic mean of the collective thermal points at which locomotory activity becomes disorganised and the animal loses its ability to escape from conditions that will promptly lead to its death" and modified it to include "when heated from a previous acclimation temperature at a constant rate just fast enough to allow deep body temperature to follow environmental test temperatures without a significant time lag".

This definition highlights the effect of acclimation on the CTM of poikilotherms. The chief component which affects acclimation is temperature but photoperiod can also have an effect (Hutchison and Kosh, 1965).

In this study the tortoises were acclimated for at least two weeks in water at 14°, 21° or 28°C and subjected to a 12 hour photoperiod. During this time they were fed weekly on minced meat.

The method of testing the CTM was based on that of Hutchison and Kosh (1965). The body temperature was monitored by a thermistor which was inserted deep into the cloaca and taped into place. The tortoise was placed in a bowl containing water at the acclimation temperature. The water temperature was then raised steadily and maintained about 5°C above the body temperature of the tortoise. Hutchison and Kosh (op. cit.) raised the water temperature at a rate high enough to raise the body temperature by 1°C per minute, but this was not practicable with the larger tortoises, since too great a difference between water temperature and body temperature would have resulted.

The temperature at which the tortoise abruptly went into spasms was recorded as the thermal point. It was characterised by a stiffening and shaking of the limbs, withdrawal of the neck and gaping of the mouth. During the later stages of heating it was necessary to hold the

tortoise's head above the surface to prevent it swallowing water due to panting. Immediately the critical point was reached the tortoise was placed in cold water to revive.

5.42 Results

The critical thermal maxima of Chelodina oblonga and C. steindachneri are plotted in Figure 23. It can be seen that there is a significant difference between the two species, the desert adapted C. steindachneri having a higher CTM. The effect of acclimation on the CTM can also be seen.

The wide range of figures obtained for C. oblonga may be due to the lack of an obvious critical point in this species. Spasms were very hard to detect in some individuals and heating was carried past the thermal point in early experiments. In later experiments, if no spasms were seen, the CTM was taken as the point at which the limbs became stiff.

The C. oblonga tested were almost all larger than the C. steindachneri (mean weights 860 gm and 320 gm). However, two or three C. oblonga were close to the weight range of C. steindachneri and two overlapped it, so weight differences cannot account for all the difference between the species.

Three other species were also tested after being acclimated at 14°C. Their CTM were as follows:

Species	number	CTM
C. longicollis	2	40.5°, 40.9°
C. expansa	1	39.4°
E. kreffti	1	39.9°

These figures are within the range obtained for C. oblonga. In addition three Pseudemydura umbrina were tested, but they were only acclimated for four days at 14°C, being almost straight from the field. They would probably have been subjected to a mean temperature of about 18° to 20°C previous to capture. Their CTM were 42.5°, 42.8° and 43.0°C. These figures overlap the range of C. steindachneri acclimated to 14°C, and the mean of 42.7° suggests that P. umbrina also has an elevated CTM. Hutchison and Kosh (1965) showed that acclimation in Chrysemys picta was complete within approximately six days, so if the same applies to P. umbrina, its actual CTM after acclimation to 14°C may be a little lower than was recorded, but not as low as C. oblonga and the other species tested.

5.5 DISCUSSION

It has been shown in the preceding sections that C. steindachneri differs markedly from C. oblonga in its ability to withstand the conditions of a desert environment: lack of water and high temperature.

The most important factor is the very much lower desiccation rate which is further reduced as the animal goes into aestivation. Coupled with this is its ability to store water in the urinary bladder. The water is utilised as the body fluids are lost by desiccation. The amount of urine in the bladders of the tortoises in the experiments reported in Section 5.3 varied considerably and the C. steindachneri had proportionately less urine than most of the C. oblonga. However, the tortoises used in this experiment had been kept in captivity for some time and would not be under the same conditions as one living in a pond about to dry up. Tortoises in such a situation would probably fill the bladder before leaving the water and going into aestivation. Residents in north-west Australia have reported finding C. steindachneri walking across country some considerable distance from water. These animals always urinate copiously when handled suggesting that they have also filled their lateral bladders before leaving the water. Tortoises used for experimentation had these bladders empty, because of this habit of emptying them when handled, but

there is no reason why they should not be used as a water store in nature. They could function in a similar manner to the urinary bladder or the water could be passed into the cloaca to be absorbed there, or even passed to the median bladder. C. steindachneri also differs from C. oblonga in possessing a bilobed urinary bladder instead of a unilobed one and this may be a way of increasing the volume of urine stored, as well as the surface area for absorption.

C. steindachneri can also convert ammonia to urates more effectively than C. oblonga and this has obvious advantages because of the toxicity of ammonia. There is, in addition, the suggestion that it can maintain its blood volume as it dehydrates, preventing the overloading of the heart due to increased viscosity of the circulating fluid. These differences are consistent with C. steindachneri being able to withstand a greater amount of dehydration than C. oblonga.

Furthermore, C. steindachneri has a higher critical thermal maximum, a great advantage to an animal living in a hot, arid climate.

This preliminary study of the water, electrolyte and nitrogen balance in two species of Chelodina highlights the physiological differences which may occur between closely related species inhabiting very different environments.

Further study of C. steindachneri would be rewarding.

The study also highlights the correlation of the physiology of the various species, especially desiccation rates, with their distribution. It is particularly noticeable that Pseudemydura umbrina, which habitually spends six months of each year out of the water, has a desiccation rate almost as low as C. steindachneri.

6.0 THE EVOLUTION OF THE CHELIDAE IN AUSTRALIA AND NEW GUINEA

6.1 INTRODUCTION

The purpose of this section is to document the relationships within the Australian Chelidae and, in particular, to discuss the origin and present distribution of *Pseudemydura umbrina*.

As previously mentioned the systematics of the Chelidae of Australia and New Guinea have not been well documented. Wermuth and Mertens (1961) listed 19 species while Worrell (1963), who considered only Australia, listed 11 species. The only major revision of the group since Boulenger (1889) is that of Goode (1967). It is proposed to use his classification as a basis for these studies. Goode lists the following species:

Chelodina longicollis (Shaw, 1793)
Chelodina novae-guineae Boulenger, 1888
Chelodina steindachneri Siebenrock, 1914
Chelodina expansa Gray, 1856
Chelodina oblonga Gray, 1841
Chelodina siebenrocki Werner, 1901
Elseya dentata (Gray, 1863)
Elseya latisternum Gray, 1867
Elseya novae-guineae (Meyer, 1874)
Emydura macquaria (Cuvier, 1826)
Emydura krefftii (Gray, 1871)
Emydura australis (Gray, 1841)
Pseudemydura umbrina Siebenrock, 1901

Goode divides Chelodina into two groups, the first containing C. longicollis, C. novae-guineae and C. steindachneri and the second the other three species. He also suggests that Emydura australis should be set apart from the other species of Emydura.

In his checklist Goode has synonymised Chelodina rugosa Ogilby, 1890 with C. siebenrocki Werner, 1901, although the former name has precedence. The type locality of C. rugosa is Cape York, Australia, while that of C. siebenrocki is New Guinea. Consistent, if minor, differences occur between these two taxa and they will be considered here as separate species. In addition, live specimens, exactly fitting the description of Emydura subglobosa (Krefft, 1876) from New Guinea, have been handled and this will be considered as a separate species from E. kreffti, which occurs in Australia.

Traditionally, the classification of Testudines has been based on morphological characters, particularly the osteology of the shell and skull and the pattern and shape of the scutes on the carapace and plastron. While these characters are very useful in distinguishing genera and sometimes species, it is often very difficult to separate closely related species because of the variability, especially in the carapace and plastron, within one species. It is particularly difficult if only a limited collection can be examined or if a single fossil is being assigned. The

former is the case with the Australian Chelidae. However, the purpose here is to consider the relationships within the family, not to delineate the various species. Towards this end biochemical methods are available to supplement morphology.

One of these methods is serology, which is the study of antigens, antibodies and the reactions between them. Three main approaches to systematic serology are evident.

1. Electrophoresis. This involves the separation of serum proteins in an electric field (for example, Smithies, 1959). Strictly speaking, this is not serology, but this technique has been used widely to show differences in the blood proteins, both within and between populations. Zweig and Crenshaw (1957), Crenshaw (1962, 1965), Friar (1964) and Ernst (1967) have applied this technique to studies of Testudine systematics.
2. Agglutination. In vertebrates this involves the agglutination of blood cells using a variety of reagents such as plant extracts or normal sera. Friar (1963) has shown differences between turtle species and individuals using this technique.
3. Precipitation. This involves the preparation of antisera and the measurement of reaction strength when they are mixed with other sera. This can be

done in a variety of ways, such as allowing a serum and antiserum to diffuse towards each other in starch-gel, usually after some separation of each by electrophoresis (immunoelectrophoresis), or mixing the serum and antiserum in a fluid medium and measuring turbidity (nephelometry). Friar (1964) has used nephelometry to examine the relationships of a number of Testudine families.

The first two of these techniques frequently show up differences within populations as well as between them, so in this study precipitation techniques were employed, since only one or two specimens of most species could be obtained.

6.2 MORPHOLOGY

6.21 Carapace

The patterns of the carapace scutes of the various species are very similar to each other, as well as to some of the South American genera, so this is of little use when comparing the differences between species.

The presence or absence of the nuchal scute has been used to categorise species or even genera. It is, however, not a good character since it may be present or absent in a single species. Normally, if a large number of specimens

is handled, one condition will be found to predominate. C. steindachneri, for example, typically has a nuchal but occasional specimens lack it. Similarly, species of the genus Elseya usually lack a nuchal but some specimens possess one.

The pattern of the bony plates is also very similar, except in one species as below.

It has been said that the Australian Chelidae, unlike most of the South American species, do not possess neural plates and that the costals meet in the mid-line (Waite, 1929; Zangerl, 1948; Williams, 1953). This appears to be the case in all the Australian species (for example P. umbrina, Figure 13) except C. oblonga (Figure 15). Nine shells of this species from near Perth were prepared and examined, together with a sub-fossil carapace from a cave near Augusta, 180 miles south of Perth. The number of neurals was as follows:

No. of neurals	No. of specimens
5	1
6	3
7	4
8	2

Thus, C. oblonga possesses a number of neurals, varying from five to eight. The specimen figured has eight. Those with fewer lack one or more of the most anterior and the two most posterior. A report that C. oblonga does not have neurals (Zangerl, 1948, p.41) is therefore incorrect. This author probably examined a specimen of C. rugosa from northern Australia or C. siebenrocki from New Guinea. These species have been incorrectly synonymised with C. oblonga in the past (for example Siebenrock, 1915; Wermuth and Mertens, 1961). Examination of C. rugosa in the Western Australian Museum and C. siebenrocki in the Australian Museum, has shown that they do not have neurals.

6.22 Plastron

The arrangement of the scutes on the plastron is much more variable and significant than on the carapace. The arrangement of the intergular in relation to the gulars and humerals is particularly important. In Elseya and Emydura the intergular is small and marginal and extends far enough inwards only to partially separate the humerals. The intergular of Elseya is usually smaller and more rectangular than that of Emydura which is dilated at the inner end. Pseudemydura has a much larger intergular than these two genera. Also, it extends inwards to completely separate the humerals and partially separate the pectorals (Figure 14).

The intergular of Chelodina (Figure 16) is similar in size and in the way it divides the pectorals, but it is completely enclosed anteriorly by the gulars and humerals. In some specimens of C. rugosa, such as C. intergularis Fry, 1915, the front end of the intergular is marginal.

The arrangement of the bony plates is the same for all four genera (Figures 14 and 16).

6.23 Skull

The skulls of the following species were examined: Chelodina oblonga, C. expansa, C. longicollis, C. steindachneri, Elseya latisternum, Emydura macquaria and Pseudemydura umbrina.

The general arrangement and shape of the various elements is very similar and the chief difference is in the type and amount of temporal emargination.

Pseudemydura umbrina (Figure 17) has no emargination from behind and has little ventral emargination so that the parietal is just in contact with the quadrate and broadly in contact with the squamosal. The supraoccipital makes up a large part of the skull roof and is broadly in contact with the squamosal.

Elseya (Figure 19) and Emydura (Figure 18), which have very similar skulls, have extensive posterior and ventral emargination. The connection between the supraoccipital and squamosal is lost and the contact between the supraoccipital

and the parietal is much reduced. Similarly there is no contact between the parietal and quadrate and the contact between the parietal and squamosal is reduced to a narrow bar.

In Chelodina (Figure 20) the posterior and ventral emarginations have joined and all contact between the parietal and squamosal has been lost. The parietals, and particularly the supraoccipital, are much reduced dorsally.

Some differences in the layout of the skull elements are also evident, particularly between Pseudemydura and the other three genera. In Pseudemydura the forward growth of the frontal does not separate the nasals, while in the other genera the separation is almost complete. Also, the premaxillae of Pseudemydura are much reduced, compared with the other genera.

Some minor differences are evident between the skulls of Elseya latisternum and Emydura macquaria. The snout of E. latisternum is more elongated and the frontals are narrower and extend further forward. Emargination has proceeded slightly further in E. macquaria and the parieto-squamosal bar is smaller. However, it is not known whether these differences occur in all species of each genus, or whether other specimens of either species are similar to the ones figured.

In Chelodina the frontals are fused and the maxillae have extended upwards so that they are in contact with the frontal and break the contact between the prefrontals and nasals.

6.24 Mandible

The mandibles of C. oblonga, C. expansa, C. longicollis, Elseya latisternum and P. umbrina were examined in detail. The only mandible of E. macquaria which was examined was incomplete.

There is little difference in the pattern of the seven bones which make up the mandible. All species examined showed well developed splenials and coronoids. The coronoid of Chelodina is visible on the outside of the mandible, unlike that of Elseya and Pseudemydura. P. umbrina differs from the other species by having a much reduced angular. In addition, the mandible which was examined showed evidence of possessing a second coronoid on the outside of the coronoid process. There is also a slight impression of this extra bone on the mandible of Elseya but not on Chelodina. The prearticular in P. umbrina, unlike that of the other species, extends forward to separate the coronoid and splenial.

6.25 Other Characters

Various other characters in the externals and general appearance of the different species have been used to separate them. These include the general shape and colour

of the animal and presence or absence of barbels and tubercles. However, while these characters may be useful in determining species, they appear to be of little value in understanding the evolution of the group.

6.26 Discussion

It is immediately evident that three very diverse groups exist within the Australian Chelidae. Emydura and Elseya make up the first group which is typified by having short necks, a small, marginal intergular and a narrow parieto-squamosal bar in the skull. The second group is made up of the genus Chelodina, members of which typically have long necks, an enclosed intergular and no parieto-squamosal bar. Pseudemydura umbrina makes up the third group. It has a short neck, a large, marginal intergular and a completely roofed skull which shows little emargination.

Within the first two groups minor groupings are evident:

	Elseya	Emydura
intergular	narrow, rectangular	broad, dilated posteriorly
nuchal	usually absent	usually present
skull cap	horny plate	smooth skin
snout	prominent	flattened
tubercles behind eye	few, prominent, large	many, flattened, small

Boulenger (1889) defined the genus Elseya as having a median alveolar ridge in the skull. This character is possessed only by Elseya dentata and Boulenger considered that E. latisternum and E. novae-guineae belonged to Emydura. Gray (1867) originally placed E. latisternum in Elseya but E. novae-guineae has been associated with Emydura until Goode (1967) relocated it. The presence or absence of an alveolar ridge is usually considered a minor character and, when compared with the other evidence above, it does not signify generic status.

Similarly, it is possible to divide Chelodina into three groups as follows:

1. Chelodina longicollis
   Chelodina novae-guineae
   Chelodina steindachneri

2. Chelodina expansa
   Chelodina rugosa
   Chelodina siebenrocki

3. Chelodina oblonga

They differ as follows:

	C. longicollis species group	C. expansa species group	C. oblonga
neck	comparatively short, thin	very long, thick	very long, thick
shape of skull	small, not flattened width/height at rear of maxillae $<1:2.5$	large, flattened width/height $>1:2.5$	large, flattened width/height $>1:2.5$
carapace length of adult female	<25 cm	>25 cm	>25 cm
neurals in carapace	absent	absent	present 5-8

C. oblonga could be placed in the second group, but the presence of neurals in this species suggests that it has been isolated from them for some time. Also, the shell of the C. expansa group is deeper and more heavily built.

Discussion of the relationships of the above groups will be delayed until the serological evidence has been considered.

6.3 SEROLOGY

6.31 Methods

The methods used were those of Kirsch (1967).

Blood was obtained by cardiac puncture using disposable plastic syringes rinsed with heparin. The blood was centrifuged at 3,000 rpm for 15 minutes and the plasma was removed with a Pasteur pipette and stored at -20°C until used.

Although the materials studied were in fact plasmas the terms serum and plasma are hereafter used interchangeably.

Antisera were produced in rabbits (New Zealand Whites) by Freund's (1956) adjuvant technique, using complete adjuvant (Commonwealth Serum Laboratories, Melbourne, Victoria). An initial injection of 1 ml of whole serum emulsified with an equal amount of adjuvant was given, followed by a rest period of three weeks and a series of three, weekly injections

similar to the first. Each injection was given subcutaneously, the whole aliquot in one site, but a different site was used for each injection. At the conclusion of the series the rabbits were rested for a week and then bled for preliminary testing. If the antiserum was satisfactory the rabbit was bled on alternate days for a week, 50 to 60 ml at a time, from a marginal ear vein and then bled out by cardiac puncture. The antisera were separated from the clot by centrifugation and stored at -20°C.

Immunoelectrophoresis (IEP) was performed according to the micromodification of Scheideggar (as described by Hirschfield, 1960). The agar used was Oxoid Ionagar No. 2 made up to 1% in pH 8.6 Veronal buffer (Hirschfield, 1960) and 2 ml was pipetted hot on to each slide. The conditions of electrophoresis were 8 to 9 v/cm for 45 minutes. Incubation was for two days at 20°C, after which the slides were washed for one day in two changes of normal saline, rinsed for one hour in distilled water and then dried under lintless filter paper at 60°C. The precipitin patterns were stained for 30 minutes in Azocarmine B (a saturated solution in 50 volumes methyl alcohol, 40 volumes water and 10 volumes acetic acid), and differentiated in the solvent until the background was colourless.

The major part of the experimental work reported here involved the standard serological technique of absorbing the antiserum with a heterologous antigen. Three or four parts of antiserum were mixed with one part antigen and the mixture incubated for 45 to 60 minutes at 37°C and overnight in the refrigerator. The precipitate was separated by centrifuging at 3,000 rpm for 15 minutes and the supernatant was pipetted off for use. The antiserum was divided into aliquots each of which was absorbed with a different heterologous set and reacted with the series of sera under consideration. The reactions were scored separately for each aliquot and expressed as a ratio, representing the number of lines in the heterologous pattern divided by the number of lines in the homologous pattern times 100. The per cent reaction was recorded on a scale of zero to five, zero being the negative reaction and five the homologous, with four equal intervals (1 to 24, 25 to 49, 50 to 74 and 75 to 99) in between. Because of the low number of lines usually involved these numbers seemed to correspond to discreet intervals and few borderline cases were noted.

A difficulty with this method of scoring is that, when absorption is performed with a serum which is very similar to the homologous antigen mixture, absorption may be complete and the homologous reaction zero. Hence the ratio is 0/0, which is undefined. It seems common sense to call such a

reaction 0% even though this is not logically correct. Kirsch (1967) subjected data containing this anomaly to the numerical analysis described below, both with and without the inclusion of the experiments giving the "0%" reactions, and the results were identical.

After scoring, the data were subjected to analysis by the Probabilistic Similarity Index (PSI) of Goodall (1966). Computation was performed on the IBM PDP-6, using Goodall's program (routines SIM 91, SIM 92 and SIM BF). The resulting matrix expresses the probabilities that the observed associations are due to chance and hence the smaller the values the smaller the distance between the taxa. Goodall in fact defines his PSI as the complement of the computed probability but, since the high negative exponents clearly convey the idea of small distances, this conversion was not made.

The procedure involves a number of steps. After the initial computation the matrix is inspected for the major clustering of low probabilities. The second step is the recomputation of the probabilities of association of the taxa which remain after the primary group has been removed. The removal of the largest group distinguished in the first run is necessary because high associations tend to distort the affinities of other taxa. If further groupings are evident after the second run they are eliminated and the probabilities for the remaining taxa again computed. This

continues until no more significant groupings are revealed.

The final step establishes the "grouping of the groups" and is accomplished by taking the means of the scores for all the taxa in each group for each character and treating these values as the input for a single taxon. In order to avoid decimal fractions these values are expressed as proportions of 10,000 and treated as continuous variables between 0 and 10,000.

Nephelometry measurements were made with an EEL Nephelometer head in conjunction with an EEL Unigalvo 20 galvanometer. Tripling dilutions of the antigens were made by mixing 0.75 ml whole serum with 6.75 ml of lithium hydroxide buffer pH 8.1, and transferring 2.5 ml of this mixture to a second tube containing 5 ml of buffer. This procedure was repeated for a series of 12 tubes.

The tubes were read to the nearest unit as blanks and then incubated with 1 ml each of antiserum in buffer (20% or 15%) for 90 minutes at 37°C. Each tube was then read again and the blank subtracted. Boyden (1942) curves were plotted for the results and all tests within a single antiserum were compared with the homologous reaction as percentages of the total turbidity.

Some samples of Chelodina oblonga and C. steindachneri sera were subjected to the vertical starch-gel electrophoresis technique of Smithies (1959). This showed that variation between sera from within the same taxon was minimal.

6.32 Results

6.321 Immunoelectrophoresis

The following species were used for IEP studies:

No.	Species	Locality
1.	Pseudemydura umbrina	Twin Swamps Reserve, Warbrook, W.A.
2.	Elseya latisternum	Burnett River, Gayndah, Queensland.
3.	Elseya dentata	North Johnstone River, Malanda, Queensland.
4.	Elseya novae-guineae	Lake Murray, Papua.
5.	Emydura macquaria	Patho, Murray River, Victoria.
6.	Emydura kreffti	Woodstock, north Queensland.
7.	Emydura subglobosa	Lake Murray, Papua.
8.	Emydura australis	Kalumburu, northern W.A. (same as W.A. Museum R28117)
9.	Chelodina steindachneri	Wiluna, W.A.
10.	Chelodina longicollis	Patho, Murray River, Victoria.
11.	Chelodina novae-guineae	Woodstock, north Queensland.
12.	Chelodina oblonga	Northam, W.A.
13.	Chelodina expansa	Patho, Murray River, Victoria.
14.	Chelodina ?rugosa	Kalumburu, northern W.A. (same as W.A. Museum R28118)
15.	Chelodina rugosa	Darwin, Northern Territory.
16.	Testudo graeca	Not known.

Antisera were made against numbers 2 (Elseya latisternum), 5 (Emydura macquaria) and 12 (Chelodina oblonga). The absorptions performed and the resulting reactions are listed in Tables 17 to 19. Figure 25 shows the precipitin patterns obtained from a series of absorptions with anti-2 compared with the unabsorbed patterns. The results of analysis by Goodall's (1966) method are shown in Tables 20 to 26, where the probabilities of association are given in E-form, that is, the negative or positive figure following the E indicates the power of ten to which the preceding decimal figure must be raised.

Table 20 indicates that the strongest large grouping is sera 5 to 8. Serum 5 appears to be further away from sera 7 and 8 than it is from serum 6, while sera 6, 7 and 8 appear equally close. The apparent distance of serum 5 shows up one of the errors which may arise in this method of analysis, namely that, if few antisera are made, the species against which they are made will appear anomalously distant from near species because of the score of 5 usually obtained with homologous reactions. The anomaly is less marked among sera 5 to 8 because of the complete absorption of anti-5 by sera 6 and 8. Table 20 also shows affinities between sera 3 and 4 and a weaker affinity between them and serum 2, as well as a loose grouping of sera 9 to 15, especially sera 14 and 15. It is also clear that sera 2

to 8 form a loose grouping.

Table 21, which shows the affinities of the remaining sera, indicates a strong affinity between sera 3 and 4 and a weaker one between them and serum 2. Once again serum 2 is the one in the group against which an antiserum was prepared. However, the grouping is clear, although serum 2 also shows a slightly weaker, spurious affinity with serum 16. A loose grouping between sera 10 to 15, especially 14 and 15, is again evident, although serum 9 has dropped out.

Table 22 shows the affinities between serum 1 and sera 9 to 16. The only strong group is sera 14 and 15 and these were removed and the remaining probabilities recomputed. The result is shown in Table 23, which in turn shows that sera 10 and 13 are close. After these were removed no strong groupings were evident (Table 24).

The "grouping of the groups" is shown in Table 25. The groups containing serum 1, sera 2 to 4, sera 5 to 8 and serum 16 show no affinity with any other group. Serum 9 is close to sera 10+13, which in turn are close to 14+15. Sera 14+15 also show affinity with serum 11. Serum 12 shows no strong affinity for any group but appears to be fairly close to sera 9, 10+13 and 11. Serum 12 is the one in this group which had an antiserum prepared against it. A slight affinity shows between sera 1 and 16. However, this is anomalous and may be due to the fact that no antisera were

prepared against species which were closely related to either and they therefore appear to associate because of the large number of zero scores obtained by each. Also, due to the incomplete absorption of anti-2 with serum 1, a slight reaction occurred with this absorption and serum 16 (Table 17).

A new "grouping of the groups" with sera 9 to 15 grouped as well as 2 to 4 and 5 to 8, shows that no further groupings are left. It does not show any relationship between groups 2 to 4 and 5 to 8, although this is evident in Table 20.

The groups obtained are as follows:

1 *Pseudemydura umbrina*

2,3,4 *Elseya latisternum*, *E. dentata*, *E. novae-guineae*

5,6,7,8 *Emydura macquaria*, *E. kreffti*, *E. subglobosa*, *E. australis*

9-15 *Chelodina*

9 *Chelodina steindachneri*

10,13 *C. longicollis*, *C. expansa*

11 *C. novae-guineae*

12 *C. oblonga*

14,15 *C. ?rugosa*, *C. rugosa*

16 *Testudo graeca*

6.322 Nephelometry

Nephelometric measurements were made of reactions between anti-*Emydura macquaria* and anti-*Chelodina oblonga* and various plasmas. The results of the anti-*C. oblonga* reactions are given in Table 27 and some are plotted as Boyden curves in Figure 24. Negative values in the zone of antigen excess are treated as zero in the Table.

It can be seen that the three species of *Chelodina* which were tested show close affinity to *C. oblonga* and are about equidistant from it. *Pseudemydura umbrina*, *Elseya latisternum* and *Emydura macquaria* fall further away from *C. oblonga* in that order. *Testudo graeca* gives a weak reaction and shows the least affinity.

The results of the reactions with Anti-*E. macquaria* were most inconclusive because the antiserum was used in too great a strength and the curves did not drop to zero in the zone of antigen excess and therefore curve areas were not comparable. Insufficient antiserum was available for the tests to be repeated.

6.4 DISCUSSION

There is no fossil record to assist in the interpretation of the present relationships and distribution of the Chelidae, so any conclusions will have to be based on data from the living species.

The results obtained from the serological investigation largely agree with the groupings based on morphology. The most important points are that the grouping of the short-necked species, other than Pseudemydura, into two genera is confirmed and that Pseudemydura is as far from either of these as it is from Chelodina. Morphological data on Emydura and Elseya suggest that they are closely related and serology tends to confirm this.

The results within the genus Chelodina are somewhat confusing. The strongest group is that of the two northern tortoises, C. rugosa from Darwin and C. ?rugosa from Kalumburu. This is logical seeing that they might be the same species. The Kalumburu specimens differ from typical C. rugosa chiefly by having radiating markings on each scute instead of the usual longitudinal wavy grooves. The other grouping obtained, of C. longicollis and C. expansa, does not agree with morphology and, in addition, these species are sympatric.

It has often been implied that systematic serology is superior to other approaches to phylogenetic taxonomy. The basis for this argument appears to be that serological studies

usually accord well with the established taxonomy when groups whose phylogeny is well known are studied (for example, Goodman, 1963).

When serology disagrees with previous classifications it is usually assumed that they are wrong, due to the morphological data being misinterpreted because of convergence or differing rates of evolution. For instance, Leone and Weins (1956) seek to erect separate sub-orders for the Canoids and Feloids, and to include the Pinnipedia within the Canoids, although ecological and morphological evidence is to the contrary. They do not consider the possibility that the serological characters have undergone convergence or that there have been differing rates of evolution. There is, however, evidence that antigens can, like any other character upon which natural selection acts, undergo convergent evolution. Damien (1964) suggests that antigen sharing by parasites and their hosts can be explained by convergence. This may be considered a special case, but other data can be interpreted as convergence, for example Zuckerkandl (1963) shows that, from the point of view of haemoglobin structure, the gorilla is just an abnormal human or vice versa, and the two species form one continuous population. Kirsch (1967), in an exhaustive study of the comparative serology of marsupials, produced evidence which could only be explained by convergence.

Many other works, such as that of Leone and Weins (op. cit.), can just as well be explained by convergence as not.

Simpson (1964) suggests that convergence to the point of identity or seriously confusing similarity would appear to be more likely in a single kind of molecule than in phyletic characters, which are the end results of the interactions of a very large number of such molecules. He concludes that no one kind of evidence on evolution is superior and that no one kind suffices in itself.

Thus, serological evidence on the phylogeny of the Chelidae must be considered with all other available information, morphological and biological.

The antiserum produced against a Chelodina was against C. oblonga, a species which, because of its unique (for Australia) possession of neurals, must have been isolated from other Chelodina for a considerable period of time. This could have the effect of making the other species appear equidistant from it, and any convergence would be highlighted. The nephelometric experiments confirm that species of both groups of Chelodina are equidistant from C. oblonga. Ideally, the IEP experiments should be repeated using antisera against more typical members of the two other groups.

Zoogeographic evidence is also useful in the interpretation of relationships.

When the distribution of the various species is plotted a number of discrete regions emerge (Figure 26, Table 28). The distribution is not well documented but the pattern displayed is interesting.

Five main regions are evident - west, south-west, south-east, north and New Guinea. The south-east and north are further divisible, the former by the Great Dividing Range and the latter at the Gulf of Carpentaria into north-east and north-west.

The south-west is isolated from the rest of Australia by areas of waterless desert and the fauna reflects this. The region is noted for its high proportion of endemic species and the two tortoises, Pseudemydura umbrina and Chelodina oblonga, are specialised and have no near relatives.

The south-east, north and New Guinea have at least one representative of each of the other groups. This appears consistent with the hypothesis that the ancestral species of each group was widespread throughout eastern and northern Australia during a period when the climate was wetter than at present, and that the species have been isolated by conditions becoming drier. The presence of Emydura sp. (probably macquaria) in isolated permanent pools in central Australia supports this.

Balme and Churchill (1959) have reported a fossil flora including the beech Nothofagus and podocarps of upper Eocene

or lower Oligocene age at Coolgardie, Western Australia (31°57'S,121°11'E) and Cookson (1953) and Cookson and Pike (1953, 1954) have reported a flora of similar age containing Phyllocladus and podocarps from Pidinga (31°S, 131° 30'E) and Cootabarlow (31°S, 139°E) in South Australia. These areas now receive five to ten inches of rain per annum. Nothofagus is at present restricted to rain forests in eastern Australia and New Guinea and occurs elsewhere in the Pacific region.

This suggests that the climate of southern Australia has become drier since the late Eocene or early Oligocene and this may have been the time when the recent speciation occurred. However, it also suggests that there would have been no climatic barrier between eastern and western Australia at that time and the question arises as to why the fauna of the south-west is not more diverse. It could not have become so dry as to wipe out the species of other groups since C. oblonga is one of the least dry adapted of all.

Other animal groups also have unique species in the south-west. Two highly specialised Anurans, Myobatrachus gouldi and Metacrinia nichollsi, which occur in the moister parts of the area, have no close relatives elsewhere (Main, in press). The honey possum, Tarsipes spencerae is another example. Thus, it would appear that the south-western corner of Australia has been isolated for some considerable

time and possibly a unique Nothofagus flora existed in this area for some time after it was cut off from the east.

In the Cretaceous a sea divided Australia from the Gulf of Carpentaria in the north to the South Australian coast (Keast, 1960; see also Glaessner and Parkin, 1957; Hill and Denmead, 1960). Any land connections would have been tenuous. In the Tertiary the sea receded to the Nullabor Plain and the resulting limestones have produced a riverless and edaphic barrier since.

In this way C. oblonga would have been isolated from the eastern Chelodina before the latter diverged, firstly into two groups, and then, with the post-Oligocene drying, into species within these groups. The initial split between western and eastern Chelodina would be associated with the loss of neurals in the latter. In this case the other genera apparently lost their neurals independently. Pseudemydura also could have been isolated in the south-west at the same time and any eastern representative of this group must have become extinct, possibly because of the lack of suitable seasonal swamps. The third major group, which gave rise to Emydura and Elseya, may have been restricted to the tropics at this time.

During the Pleistocene Australia was joined to New Guinea by land bridges. These allowed the movement of rain forest frogs such as Ranids and Microhylids from New Guinea

to Australia (Straughan and Main, 1966; Main, in press) so they must have been suitable for the interchange of tortoises as well. If Chelids were isolated in New Guinea in the Oligocene they could have moved into Australia at this time. Chelodina novae-guineae, in particular, is a very wide ranging species and is known from northern Australia and Rotti, near Timor, as well as New Guinea. It could have invaded northern Australia during the Pleistocene, its movement very far south being prevented by low temperatures. The other groups have species pairs in New Guinea and northern Australia. They are Chelodina rugosa and C. siebenrocki, Emydura kreffti and E. subglobosa and Elseya nova-guineae and E. dentata. Another explanation for the New Guinea tortoises is that there were no Chelids in New Guinea until the Pleistocene and that they moved into New Guinea from northern Australia at that time. At present little information is available on the differences between the New Guinean and Australian species.

Moister conditions prevailed in southern Australia during the Pleistocene. Main, Lee and Littlejohn (1958) and Main (in press) have shown that three successive migrations of frogs from east to west occurred during the pluvials. During two of these only those frogs adapted to seasonally arid conditions were able to migrate but in one (probably the second) wet land, but not forest, species

invaded the south-west. Evidently the conditions were never wet enough for the eastern tortoises to migrate across.

Land bridges also existed between Australia and Tasmania but conditions must have been too cold for tortoises to penetrate, or survive, in Tasmania since no living tortoises are known from there.

The western region differs from the other regions in having only one species of tortoise, Chelodina steindachneri. This region is now arid and C. steindachneri has evolved special mechanisms which enable it to survive drought. This distribution is consistent with the area having been somewhat wetter in the past, probably in Oligocene time, but not wet enough for the wholly aquatic and fast dehydrating C. expansa group, Emydura or Elseya to penetrate it from the north. As the climate became drier the region lost its connection with the north and migration of C. steindachneri into the south-west would have been prevented by its preference for higher temperatures.

Another species which is restricted to this region, but which has close relatives in moister eastern Australia, is Arbanitis hoggi (Araneae). A parallel is Hyla rubella (Anura), a distinctive species which is notable for being the only Hylid widespread in arid areas. The genus has many species in warm, moist situations in northern Australia.

There are also many parallels in the plants, for example, the palm Liverstonia alfredii, Melaleuca leucodendron and Brachychiton gregori.

A diagram showing the affinities of the Chelidae of Australia and New Guinea is given in Figure 27. The barriers which caused the post-Oligocene speciation are of two sorts, physical and climatical. Emydura macquaria and E. krefftii are separated by the Great Dividing Range but E. macquaria can withstand much colder water than E. krefftii, which is not found further south than latitude 32°S. Similarly, C. longicollis and C. novae-guineae appear to be kept apart by their different temperature preferences. In the north E. australis and E. krefftii are restricted to the wetter areas while C. novae-guineae, which can withstand drought, is wide-ranging. Elseya dentata seems to have penetrated the north-east from the north-west, possibly during the Pleistocene.

The origin of the Australian Chelidae is unknown. The family is known only from this region and South America and fossils from the Northern Hemisphere, which were thought to be Chelids, have been shown to be Pelomedusids (Williams, 1953, 1954). Good sequences of fossil Pelomedusids are known from many areas in the Northern Hemisphere (Zangerl, 1948) and, assuming that they were once widespread, it seems surprising that no Chelids have been found. The alternative hypothesis, that the group developed in the Australian region and rafted to South America, therefore seems plausible.

7.0 SUMMARY AND CONCLUSIONS

Only one family of Testudines, the Chelidae, is found in Australia, and it has radiated to fill a variety of aquatic situations.

This study was aimed chiefly at understanding the limited range and rarity of Pseudemydura umbrina.

P. umbrina has a known range of a few square miles. It occurs in countable numbers only on two reserves, totalling 530 acres, which were set up for its protection and are situated between Upper Swan and Bullsbrook, 25 miles north-east of Perth, Western Australia.

It is restricted to temporary swamps on a clay or sand-over-clay soil, which normally contain water from June to November or December each year. During the dry summer and autumn months the tortoises aestivate, either in naturally occurring holes in the ground or under leaf litter or fallen branches.

Females lay three to five eggs per annum and juveniles take from seven to ten years to reach sexual maturity. Food is aquatic invertebrates and tadpoles. On the Ellen Brook Reserve, which has clay swamps totalling 14 acres, the number of tortoises is thought to be about 20. Of the 13 tortoises handled from this reserve, five (29.5%) were juveniles. On the Twin Swamps Reserve, which has about 34 acres of sand-over-clay swamps, the number is probably about 200. Seventy-nine P. umbrina were handled from this

area and 57 (73.1%) were juveniles. An examination of the age classes present on this reserve shows that the survival of hatchlings is dependent on the weather. If rainfall is low, the resulting short duration of the swamps does not allow sufficient growth of hatchlings to prevent their death by desiccation during the following summer. The swamps on the Ellen Brook Reserve normally contain water for a shorter time each year than those on the Twin Swamps Reserve and this reduces recruitment there. Other factors which affect the density of P. umbrina are fire and predators.

The distribution of suitable habitat is limited and has been further restricted by clearing and drainage. The dependence of P. umbrina on a well developed woodland for aestivation refuges prevents it using temporary water in cleared farming country and its future range will probably be restricted to the reserves.

Recommendations for the management of the reserves have been made, both for the benefit of the tortoise and for the acceptance of the reserves by nearby landholders and local authorities. It is suggested that P. umbrina should persist, at least on the Twin Swamps Reserve.

A comparative physiological study of Chelodina oblonga, which inhabits permanent water in the moist south-west corner of Australia and C. steindachneri which inhabits

temporary water-courses in the arid north-west of Western Australia was also undertaken. This was aimed partly at understanding the physiological adaptations of P. umbrina and partly at investigating some of the mechanisms which limit the distribution of all the Australian species.

The study highlighted the adaptations of C. steindachneri to a desert environment. The most important factor is a very much lower rate of water loss, particularly via the skin. Both species are able to store water in the urinary bladder, and possibly in the lateral bladders, which can be utilised when they dehydrate. However, when dehydrated, C. steindachneri is able to convert ammonia to urates more efficiently than C. oblonga. It can also control electrolyte levels in the plasma, suggesting that it can maintain its blood volume thus reducing the load on the heart. As a result of these adaptations it can withstand a greater degree of desiccation. In addition C. steindachneri has an elevated critical thermal maximum.

P. umbrina also shows physiological adaptation to its environment by having a low rate of water loss and an elevated critical thermal maximum.

When water loss rates of other Australian Chelidae are measured, it becomes apparent that most species are only able to inhabit permanent or semi-permanent water and apart from P. umbrina and C. steindachneri only C. novae-guineae,

which occurs in dry areas of northern Australia, has a very low desiccation rate.

An evolutionary study of the Chelidae, using morphological and serological data, showed that P. umbrina is a unique species and is as distantly related to Chelodina as it is to the other short-necked species. The grouping of these into two genera, Emydura and Elseya, was confirmed but they are more closely related to each other than to any other group. Chelodina oblonga was shown to possess neural plates, a unique character in the Australian Chelidae, and the remaining species of Chelodina were divided into two groups.

When the above affinities are viewed in relation to the present distribution of the family in Australia and New Guinea, and the past climates of this area, it becomes apparent that P. umbrina and C. oblonga have been isolated in the south-west for a considerable period of time, probably since the Cretaceous. It is suggested that speciation in the remaining groups has been caused by increasing aridity since the Oligocene. Pleistocene land bridges between New Guinea and Australia have allowed mixing of the northern species, but the increased rainfall in the southern half was insufficient to allow migration of the eastern species into the south-west.

Knowledge of the biology of the two south-western species throws some light on the past climate of this area since it was isolated. C. oblonga can only live in permanent water and P. umbrina is completely dependent on a Mediterranean climate with heavy winter rains. Thus the climate of this area cannot have been much drier than at present. Indeed the very restricted range of P. umbrina at the present, suggests that any further drying will cause its extinction.

Thus, P. umbrina, which has no close relatives elsewhere, has become entirely adapted to a seasonal weather pattern of heavy winter rains followed by a dry summer. It is limited by the amount of rainfall, because, if this is insufficient, hatchlings do not grow enought to survive the summer.

Finally, it is clear that although the Testudine fauna is not rich in species, it does in fact encompass a wide range of diverse adaptations and shows a complete radiation to fill the available ecological situations.

8.0 ABSTRACT

This thesis reports the results of a comprehensive study of the Australian Chelidae (Testudines, Pleurodira) undertaken to understand the limited range and rarity of Pseudemydura umbrina.

It has been shown that P. umbrina is adapted to a seasonal weather pattern of heavy winter rains followed by a warm, dry summer. It spends only six months of the year in water and is limited by the amount of rainfall, since, if this is insufficient, the swamps dry early and hatchlings do not grow enough to survive desiccation during the summer.

A comparative physiological study of P. umbrina, Chelodina oblonga, which inhabits cool permanent water and C. steindachneri which inhabits temporary water-courses in a hot arid area, highlighted the adaptations in P. umbrina and C. steindachneri to a semi-terrestrial mode of life. The most important adaptation is a reduced rate of cutaneous water loss. The distribution of other Australian Chelidae was shown to be dependent on their inability to control water loss.

Relationships based on morphology and serology show that there are four genera in Australia and New Guinea. Emydura and Elseya are closely related, but Pseudemydura is as far from them as it is from Chelodina. Within Chelodina three groups are evident, C. oblonga being unique.

The span of time involved in the evolution of the family in Australia is postulated as being from the Cretaceous to the present. The south-western species are thought to have been split off in the Cretaceous and the radiation in the other groups is probably due to a post-Oligocene drying.

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Dr. R. George read and criticized part of the manuscript.

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11.0 APPENDICES

I Radio-Tracking

II Figures

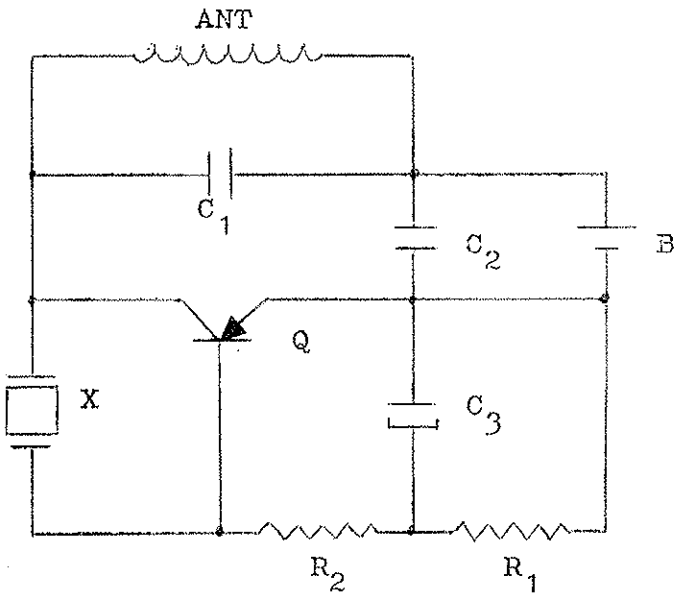
III Tables

IV Plates

APPENDIX ONE Radio-Tracking

1. Transmitter

The basic circuit is from Tester, Warner and Cochran (1964) but the individual components are as follows:



Q	Texas Instruments TI-411
X	Hc-18u 27030 - 27220 Kilocycles in 10 Kilocycle steps (AWA or STC)
B	Mallory RM12T2
R_1	150 K - 390 K
R_2	1.2 K
C_1	100 - 150 PF
C_2	0.01 μF 25 V disc ceramic
C_3	4 μF tantalum (Phillips)

The components were soldered to pins on a piece of matrix board. First a piece of copper wire was selected for the antenna so that it fitted around the rim of the carapace of the tortoise to be instrumented. After the antenna had been connected, the crystal, R_2, C_2 and C_3 were put in place together with the transistor which had previously been selected for high gain on a transistor tester. Then an ammeter was connected in series with the battery and hooked up to the other components. The value of R_2 was then selected so that the current drain was between 0.6 and 0.75 mA. R_1 and the battery were then soldered into place and the radio tuned by selecting the correct valve for C_1. This was done with the aid of a signal strength meter similar to that described by Verts (1963) but using a Phillips OA90 diode. Fine tuning could be done either by varying the length of the wires on a capacitor of nearly the right value or by adding other capacitors of low value.

The completed transmitter was then tested for underwater transmission by putting it into a plastic bag and submerging it in water. If transmission ceased the value of C_1 was increased in 5 PF stages until normal transmission occurred. This meant that the transmitter was not working at its optimum on land in most cases.

A point which was found to be important was that it was necessary to tune the circuit using a partially used

battery. The normal voltage of the mercury cells is 1.35 but, when fully charged, the voltage is often in excess of 1.4. If the circuit was tuned at the higher voltage it would not function under water when the voltage dropped.

When completed the transmitter was potted in two coats of Dow Corning Silastic RTV 589 silicone rubber. After this a thin layer of Selley's Araldite epoxy-resin was painted over the top and front of the transmitter to prevent the potting being rubbed off as the tortoise moved along. When this was dry the transmitter was glued to the carapace with 3M Adhesive EC-847. Three pieces of polyurethane plastic foam were then fashioned to fit behind and on either side of the components and also glued on to the carapace. These pieces of foam were made bigger than was necessary to restore neutral buoyancy to the tortoise and, after the glue had set, the tortoise was placed in a trough of water and pieces of foam shaved off until neutral buoyancy and normal balance were restored. The transmitter and foam were then given a further coat of glue before the tortoise was released.

The life of the transmitter at a current drain of 0.75 mA should be 4,800 hours (200 days). In practice the battery was usually changed after about 160 days, but one ran for 210 days in the field. A summary of radio-tracking data is given in Table 5.

2. Receiver

A Fonet 501 citizens' band walkie-talkie was used to locate the transmitters. It was modified by the addition of a loop aerial, a beat frequency oscillator and extra crystal banks. In the field a range of between 100 and 300 yards was obtained, depending on the transmitter and on the location of the tortoise.

The direction of the transmitter, as indicated by the null from the receiving loop, was often inaccurate. This is thought to be due partly to the unequal radiation pattern of the transmitter loop aerial and partly to the transmitter loop being horizontal instead of vertical. However, this did not affect the results because the aim was to actually locate and handle the animal and not to triangulate and compute its position from a distance.

FIGURE 1

GEOGRAPHIC DISTRIBUTION OF C. OBLONGA AND C. STEINDACHNERI IN WESTERN AUSTRALIA

SHOWING ALSO 10" ISOHYETS AND DISTRIBUTION OF CLIMATES ACCORDING TO THE THORNTHWAITE CLASSIFICATION (1931)

CB's SUBHUMID MESOTHERMAL GRASSLAND, RAINFALL DEFICIENT IN SUMMER
DB's SEMIARID MESOTHERMAL STEPPE, RAINFALL DEFICIENT IN SUMMER
EB'd ARID MESOTHERMAL DESERT, RAINFALL DEFICIENT IN ALL SEASONS
EA'd ARID TROPICAL DESERT, RAINFALL DEFICIENT IN ALL SEASONS
DA'w SEMIARID TROPICAL STEPPE, RAINFALL DEFICIENT IN WINTER

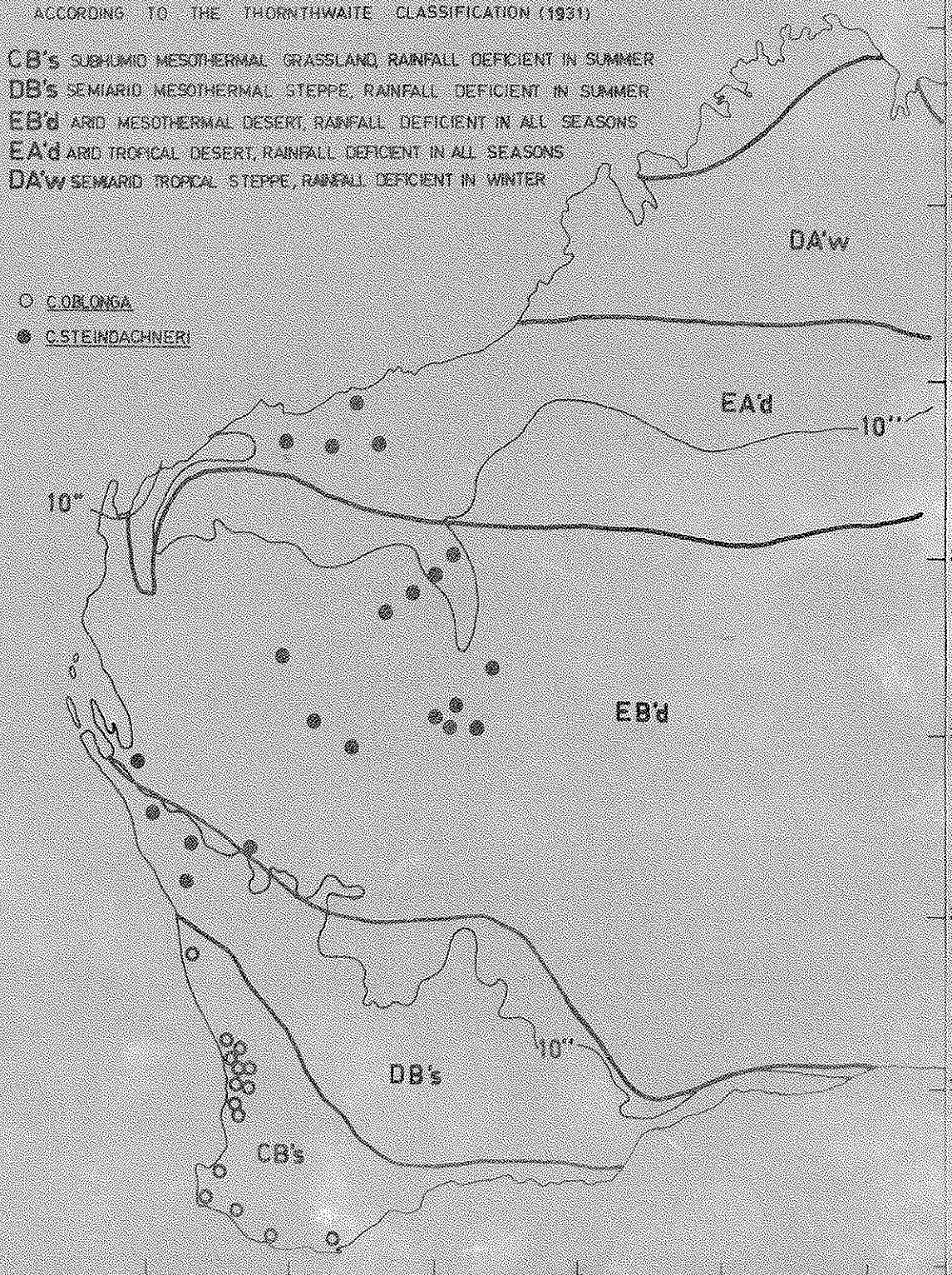
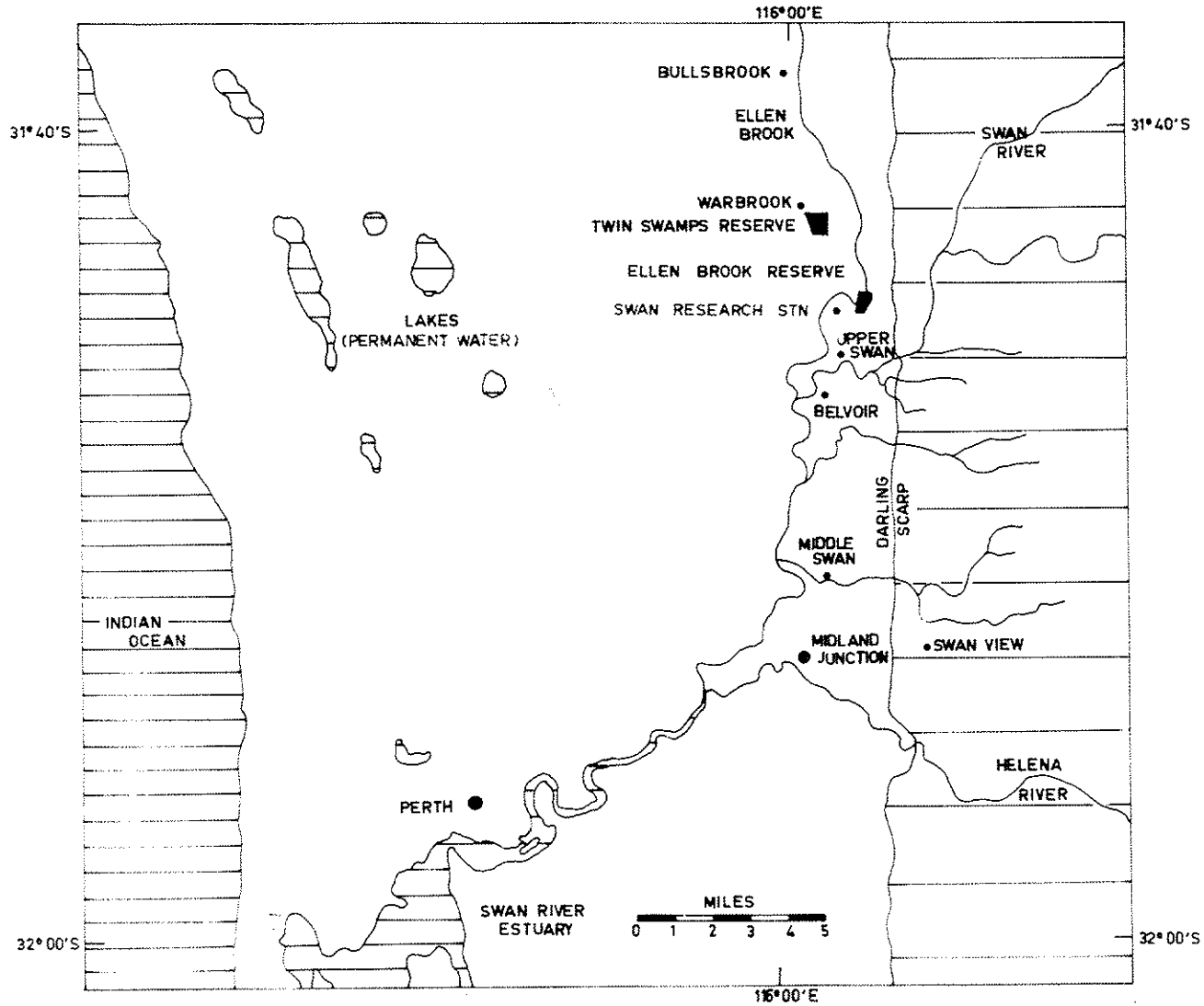


FIGURE 2

LOCALITIES NEAR PERTH



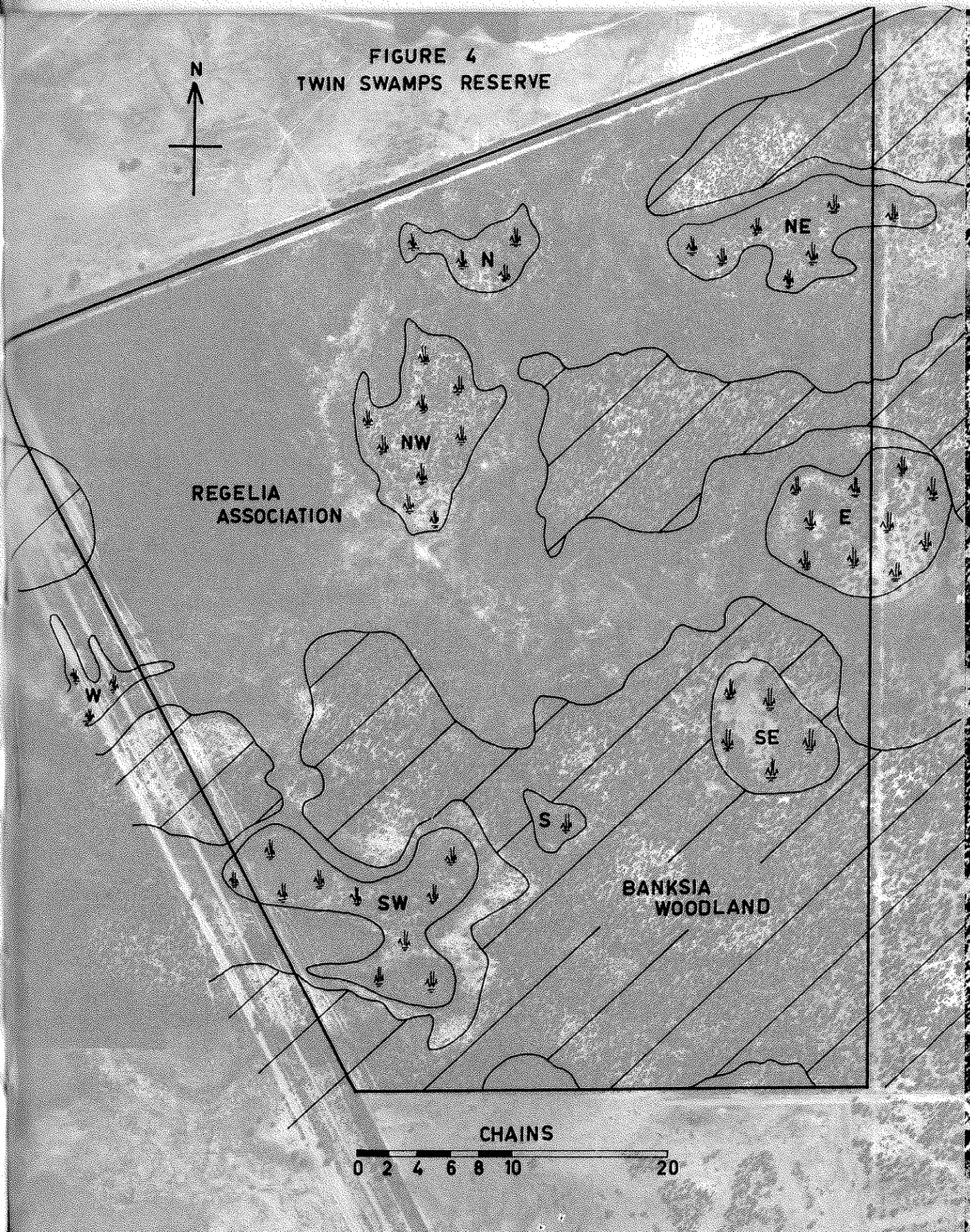


FIGURE 4
TWIN SWAMPS RESERVE
N
N
NE
NW
REGELIA
ASSOCIATION
E
W
SE
S
SW
BANKSIA
WOODLAND
CHAINS
0 2 4 6 8 10 20

FIGURE 5

RELATIONSHIP BETWEEN CARAPACE LENGTH AND CARAPACE LENGTH-WIDTH RATIO IN PUMBRINA

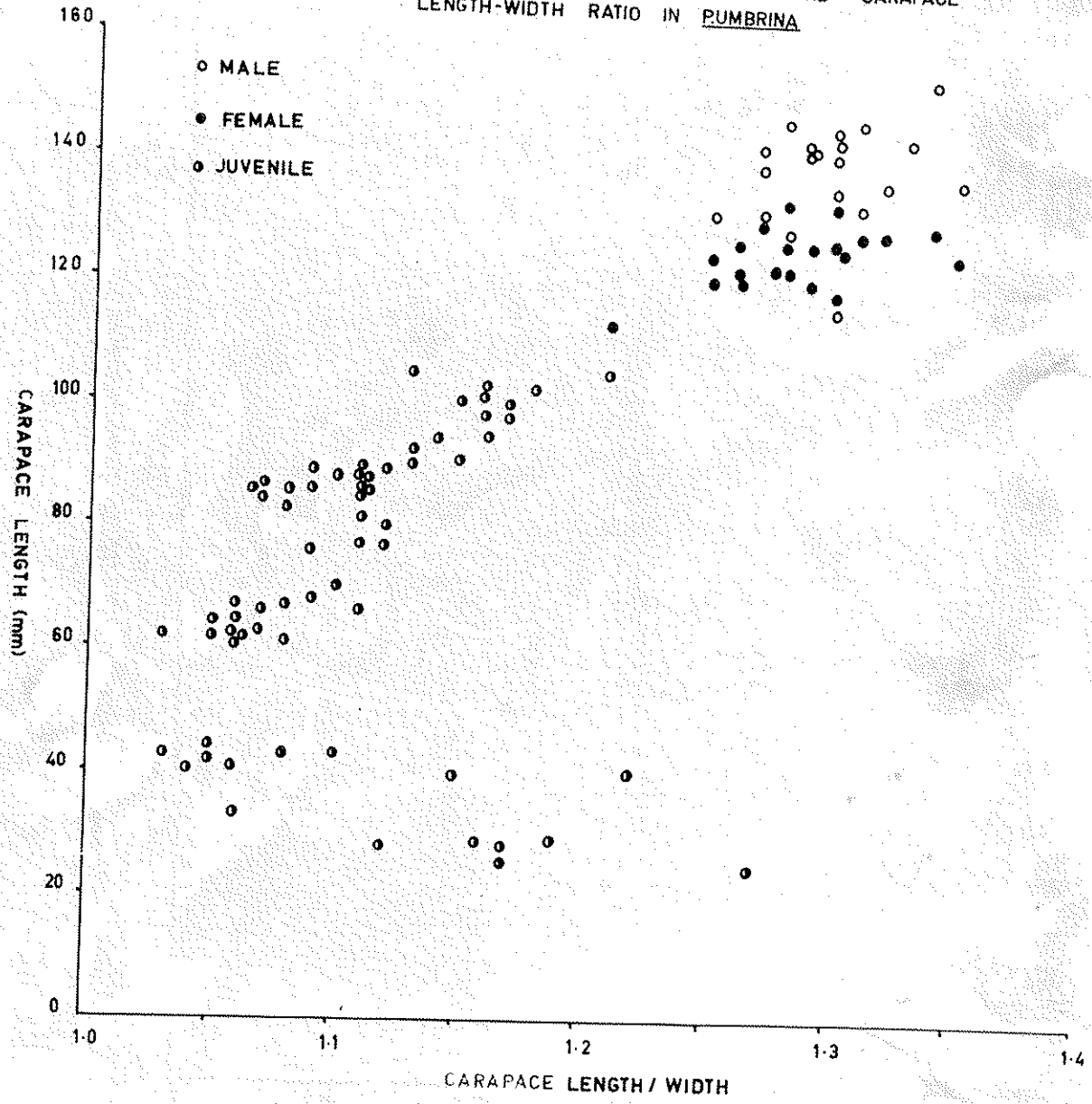


FIGURE 6

RELATIONSHIP BETWEEN CARAPACE LENGTH AND BODY WEIGHT IN P. UMBRINA

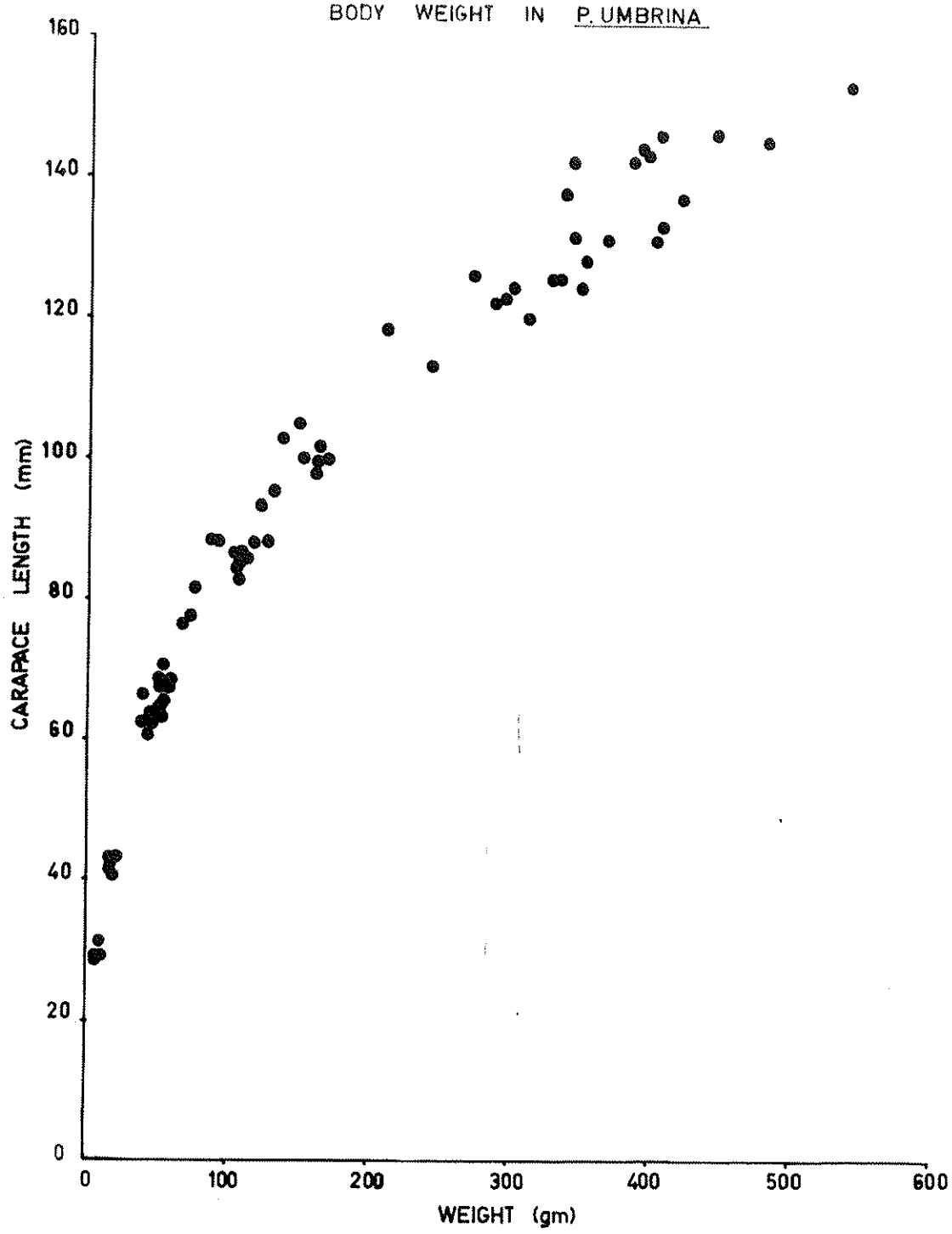


FIGURE 7

RELATIONSHIP BETWEEN CARAPACE LENGTH AND THE WIDTH OF THE FIRST VERTEBRAL SCUTE IN *P. UMBRINA*

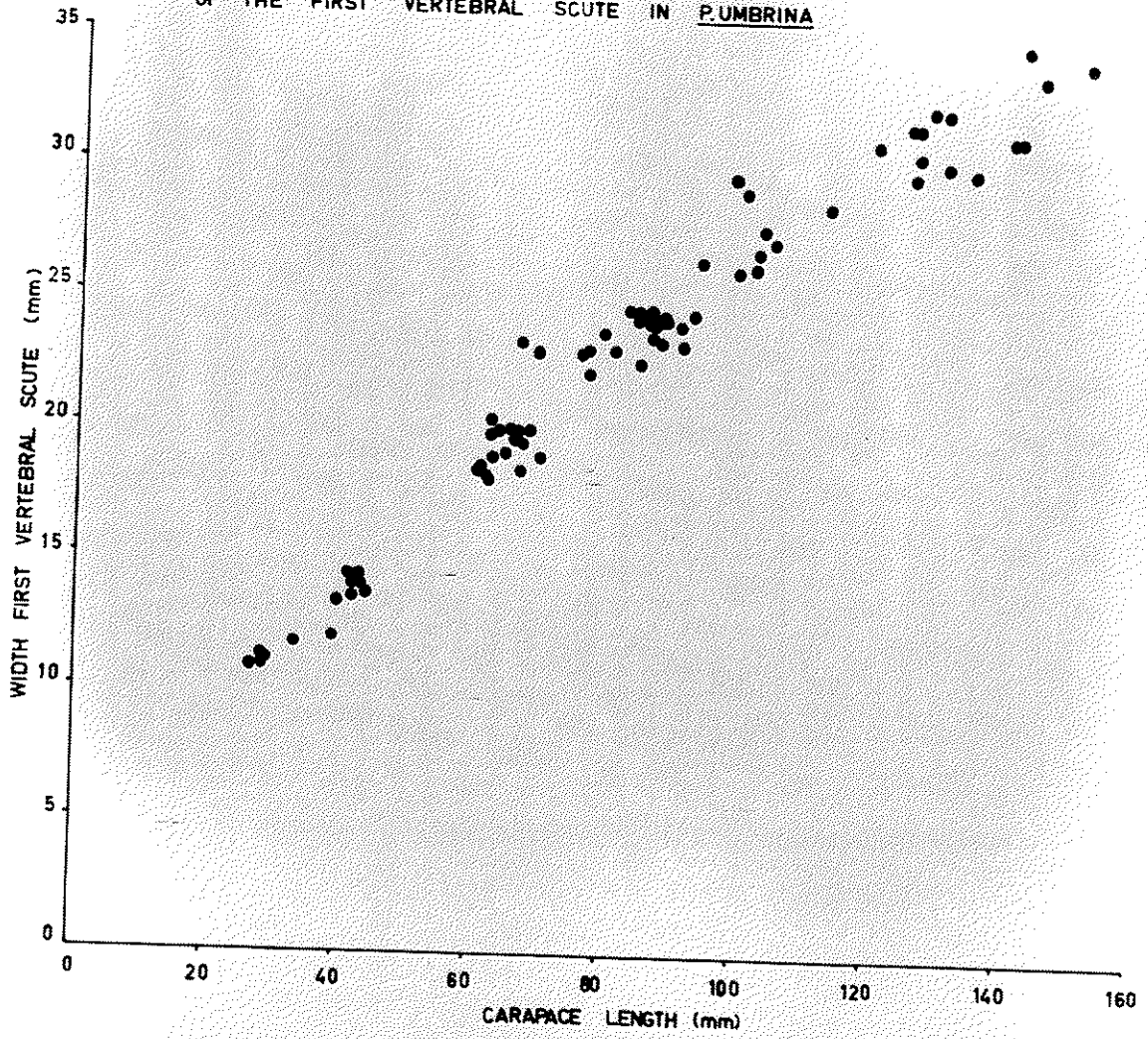


FIGURE 8

Radio-tracking. No. 21♂

1. 7. 7.65 Released NW swamp 14.7.65
2. 22. 7.65 Under clump of sedge BT 12.2° 1000 hours
3. 29. 7.65 Northern edge NW swamp, feeding BT 16.6° 1230
4. 6. 8.65 Under clump of sedge BT 12.5° 1030
5. 31. 8.65 Three inches water, Regelia association
6. 13. 9.65 SE swamp, feeding
7. 12.10.65 SE swamp
8. 26.10.65 SE swamp, removed to replace battery
9. 20.11.65 Returned to E swamp
10. 2.12.65 Back in SE swamp, BT 21.0° 1100
11. 17.12.65 SE swamp, only little water left BT 24.6° 1200
12. 26.12.65 Under Acacia cyanophylla litter signal then lost
13. 7. 7.66 Recaptured NW swamp. Released with new radio 17.7.66
14. 28. 7.66 In clump of Algae BT 15.2° Transmitter intermittent, tortoise removed to lab. released 11.8.66
15. 18. 8.66 In two inches water, active, BT 15.2° 1130
16. 8. 9.66 Under Regelia, out of water
17. 15. 9.66 Out of water
18. 22. 9.66 Out of water
19. 25.10.66 W swamp, same place until 4.11.66
20. 9.11.66 West Swamp, east of Railway
21. 18.11.66 Back on west side of Railway. 30.11.66 same place, removed to replace battery
22. 21.12.66 Swamp dry, released in Banksia woodland
23. 30.12.66 Under Phlebocarya in shade of Nuytsia
24. 5. 1.67 Under Banksia attenuata leaf litter
25. 13. 1.67-24.1.67 Under B. attenuata leaf litter, against tree trunk
26. 10. 2.67 Under Phlebocarya. Removed to check transmitter Released 13.2.67
27. 21. 2.67-11.5.67 In middle of clump of Phlebocarya in shade of Eucalyptus calophylla
28. 28. 6.67 In pit trap on west side of SE swamp

FIGURE 8

MOVEMENTS OF NO. 21♂ AS SHOWN BY RADIO TRACKING

TWIN SWAMPS RESERVE

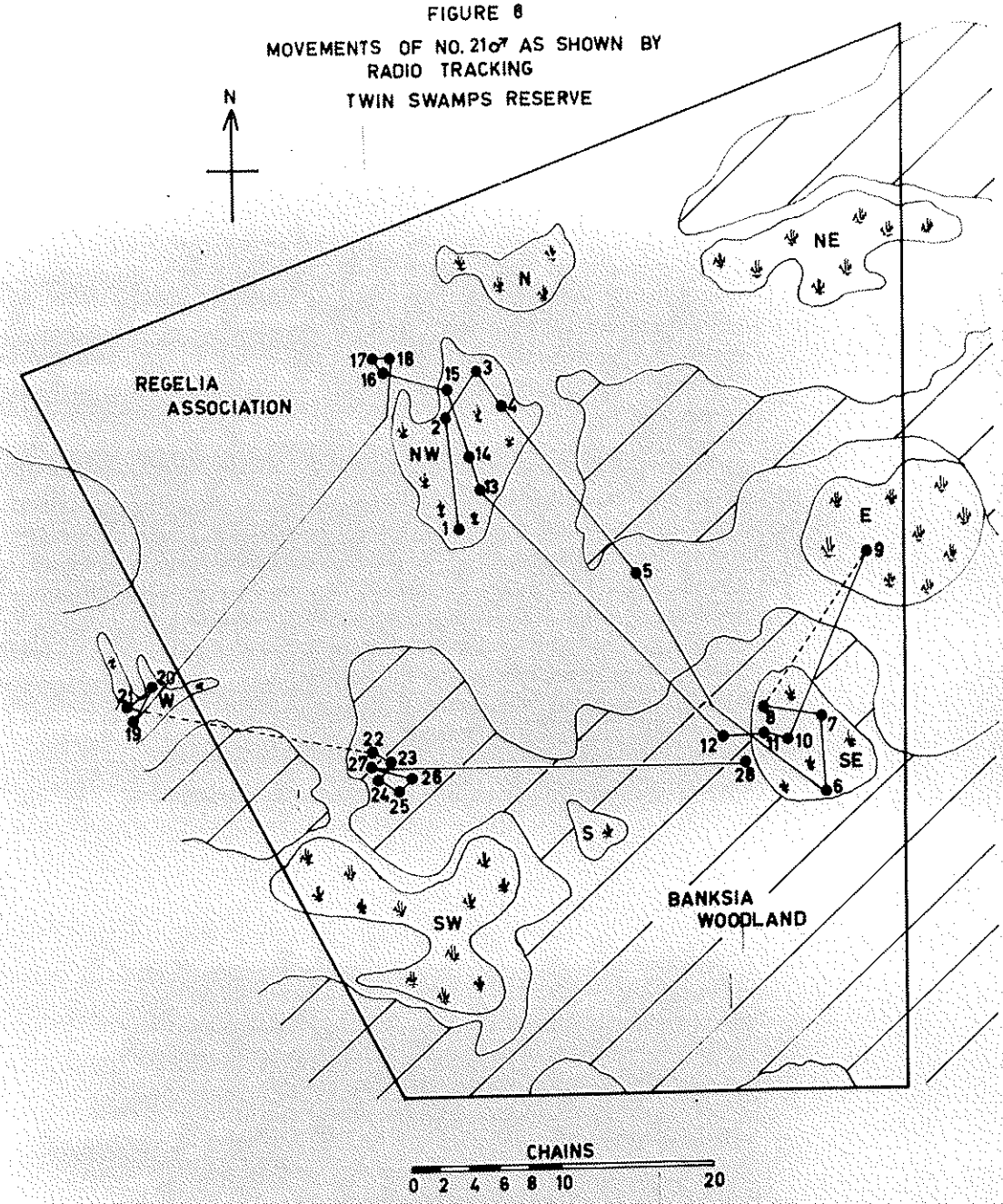


FIGURE 9

Radio-tracking

No. 40♂

1. 4. 8.66 Captured NW swamp. Released with radio 18.8.66
2. 8. 9.77 Shallow water, BT 18.0°, feeding. Similar region 15.9.66 BT 16.5°, 22.9.66 BT 17.0°
3. 6.10.66 Under low Regelia BT 17.5°. Same place until 19.10.66
4. 22.10.66 Moving south BT 24.0° 1138
5. 25.10.66 In tunnel in soil BT 17.0°, Air 27°. Same place 28.10.66
6. 1.11.66-4.11.66 In Banksia litter under Macrozamia BT 23.7° Air 25.5°
7. 9.11.66-21.12.66 Under fallen Eucalyptus Todtiana branch
8. 30.12.66-13.1.67 Under fallen Banksia attenuata branch
9. 24. 1.67-8.3.67 In tunnel in soil (same as position 5)
10. 16. 3.67 Under B. Menziesii litter against tree trunk
11. 23. 3.67 Burrowed into soil beneath fallen Melaleuca trunk. Removed to replace battery. Returned 31.3.67 6.4.67-25.5.67 Under Phlebocarya near release point
12. 1. 6.67 Under Phlebocarya and Regelia
13. 9. 6.67 Under Leptocarpus and Schoenus. Not in water
14. 16. 6.67 Swimming in SE swamp
15. 22. 6.67 Under Melaleuca raphiophylla branch
16. 29. 6.67 Under Schoenus, three inches of water BT 14.1°

No. 67♀

1. 19.10.66 Captured E swamp. 28.10.66 E swamp dry, released NW swamp
2. 1.11.66 Moving north-east in Acacia thicket
3. 4.11.66 In shallow tunnel in soil. Same place until 5.1.67
4. 13. 1.67-16.3.67 Under Banksia Menziesii litter
5. 23. 3.67 Under Acacia cyanophylla litter
6. 31. 3.67-18.4.67 Under B. attenuata litter. Removed to replace battery. Returned 27.4.67
7. 4. 5.67-17.5.67 In dense clump of Jacksonia furcellata
8. 25. 5.67 Under fallen Leptocarpus. Not in water
9. 1. 6.67 Under Jacksonia furcellata
10. 16. 6.67 In water, male attempting to copulate, BT 16.2° 1100
11. 22. 6.67 Shallow water, active

FIGURE 9

MOVEMENTS OF NOS. 40 ♂ AND 67 ♀
AS SHOWN BY RADIO TRACKING

TWIN SWAMPS RESERVE

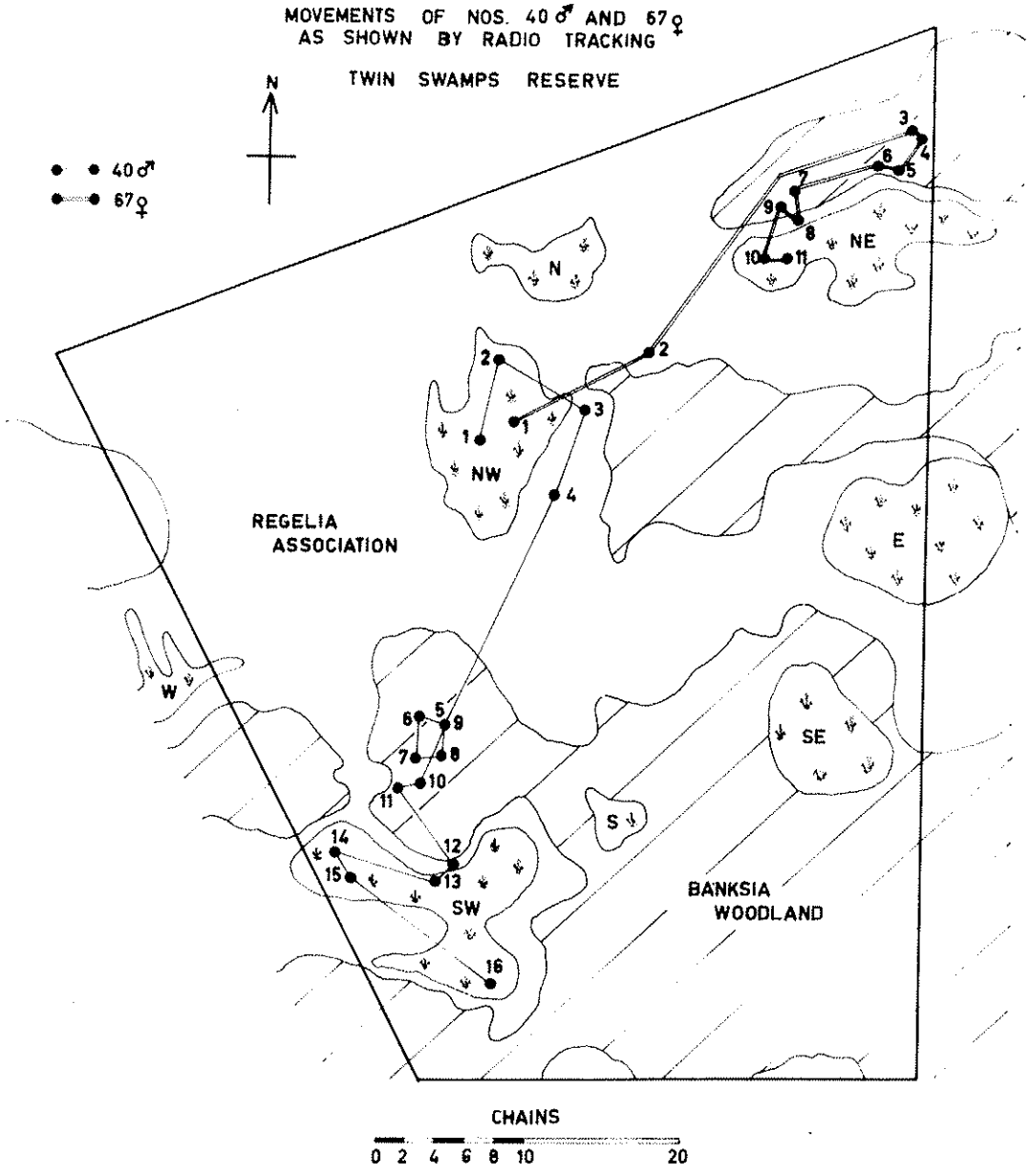


FIGURE 10

LOCATION OF P.UMBRINA THROUGH THE YEAR

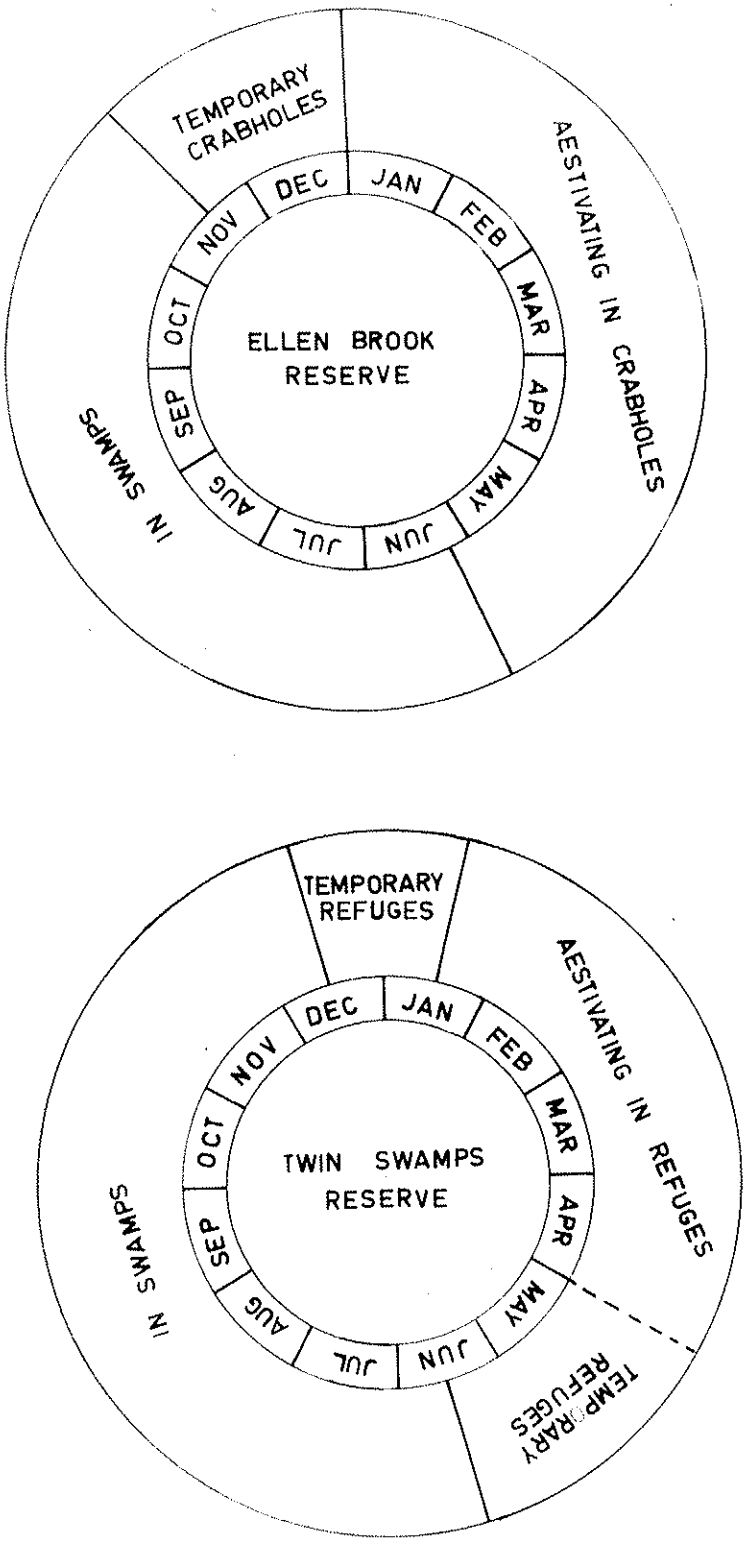


FIGURE 11

TEMPERATURE RECORDING OF THREE SITUATIONS AT THE TWIN SWAMPS RESERVE DURING THE LAST WEEK OF FEBRUARY 1967

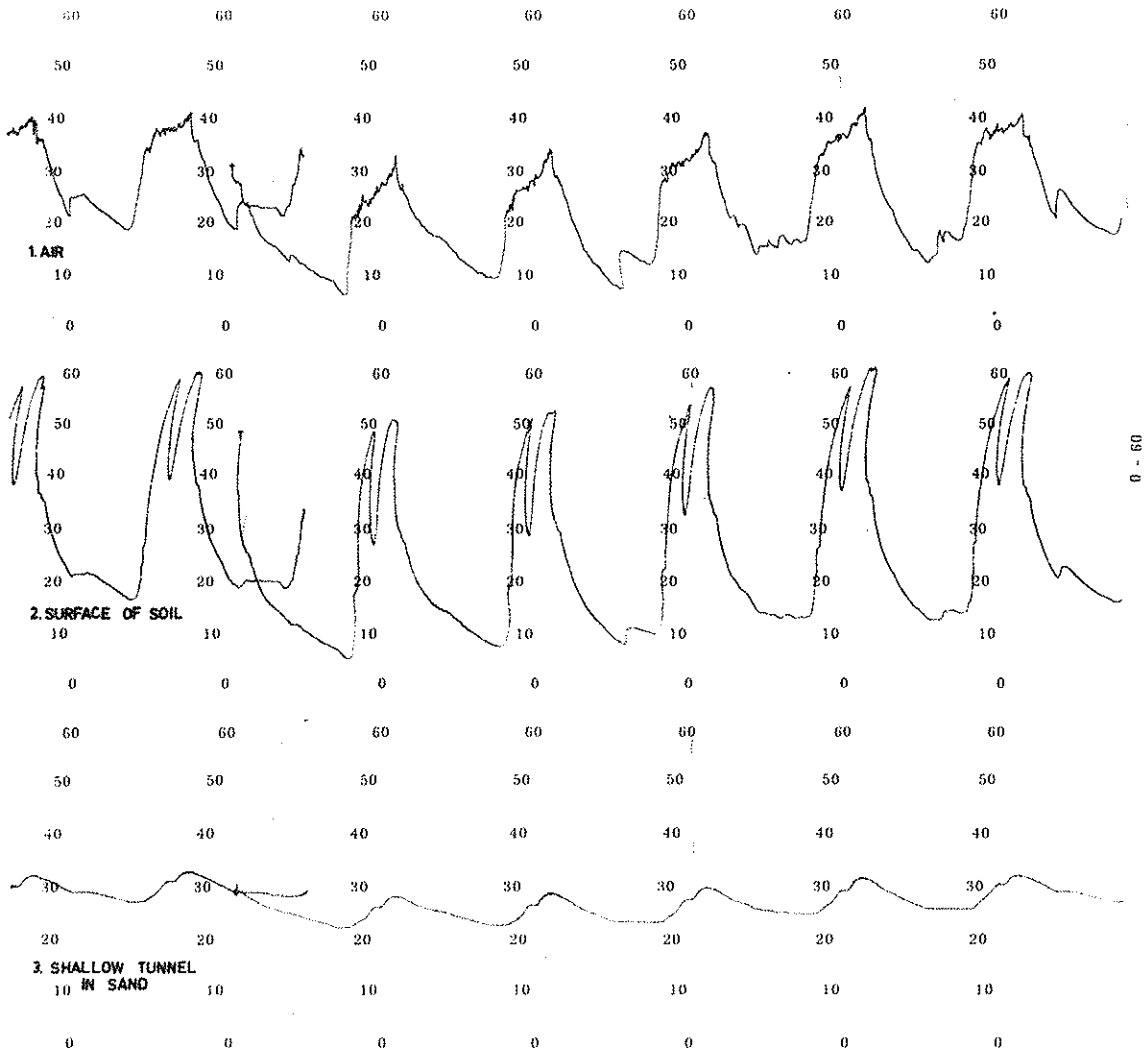
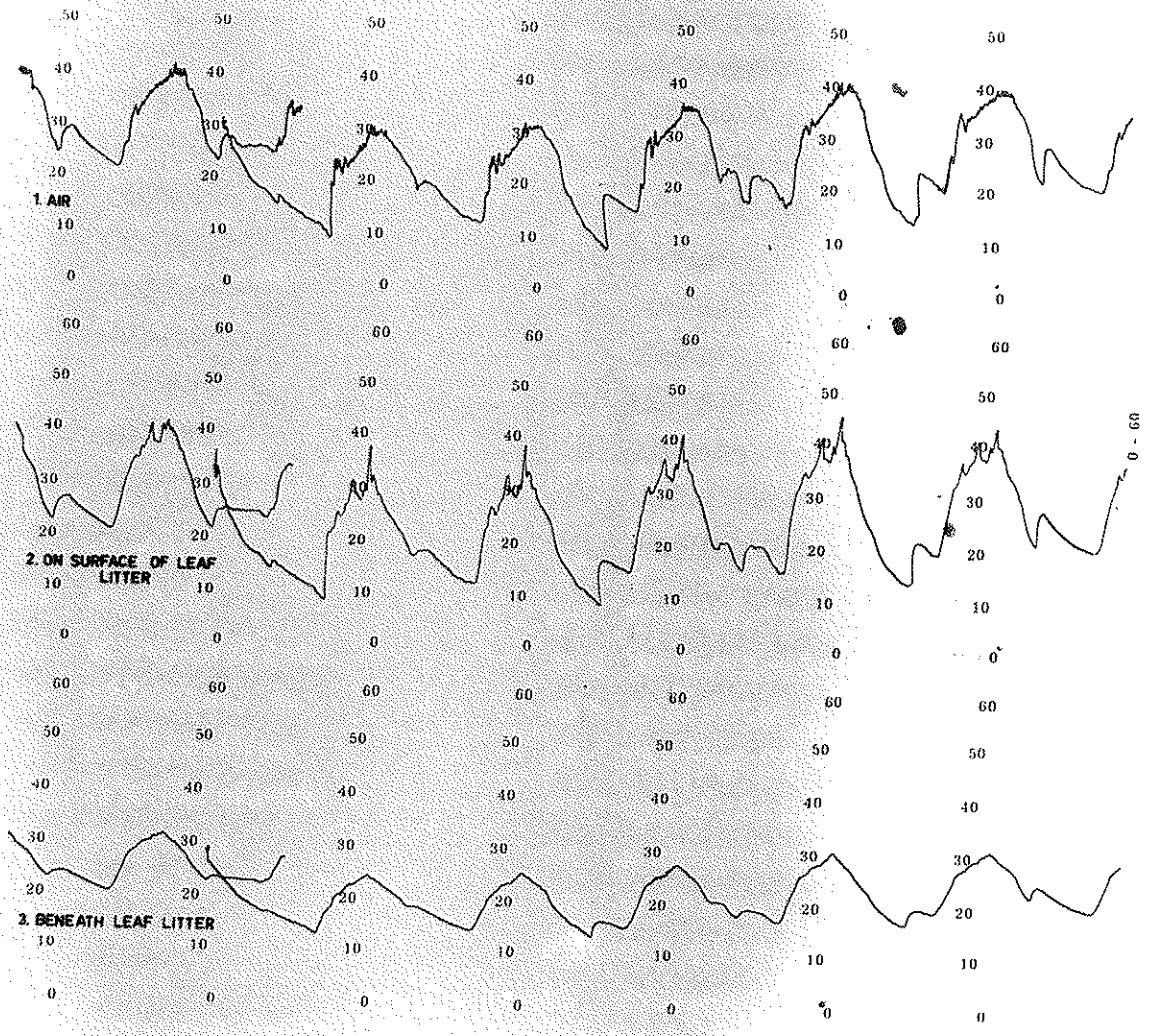


FIGURE 12

TEMPERATURE RECORDING OF THREE SITUATIONS AT THE TWIN SWAMPS RESERVE DURING THE LAST WEEK OF FEBRUARY 1967



KEY TO FIGURES 13 to 20

SHELL

Scutes

A	abdominal
AN	anal
C	costal
F	femoral
G	gular
H	humeral
I	intergular
M	marginal
N	nuchal
P	pectoral
V	vertebral

Plates

c	costal
ca	caudal
en	entoplastron
ep	epiplastron
hy	hyoplastron
hyp	hypoplastron
m	marginal
n	neural
nu	nuchal
p	pygal
x	xiphiplastron

SKULL AND MANDIBLE

a	angular
ar	articular
bo	basioccipital
c	coronoid
d	dentary
ex	exoccipital
f	frontal
j	jugal
m	maxilla
n	nasal
pal	palatine
par	parietal
pf	prefrontal
pm	premaxilla
po	postorbital
pra	prearticular
pro	pro-otic
pt	pterygoid
opi	opisthotic
sa	surangular
so	supraoccipital
sp	splenial
sq	squamosal
v	vomer

FIGURE 13

P. UMBRINA
CARAPACE

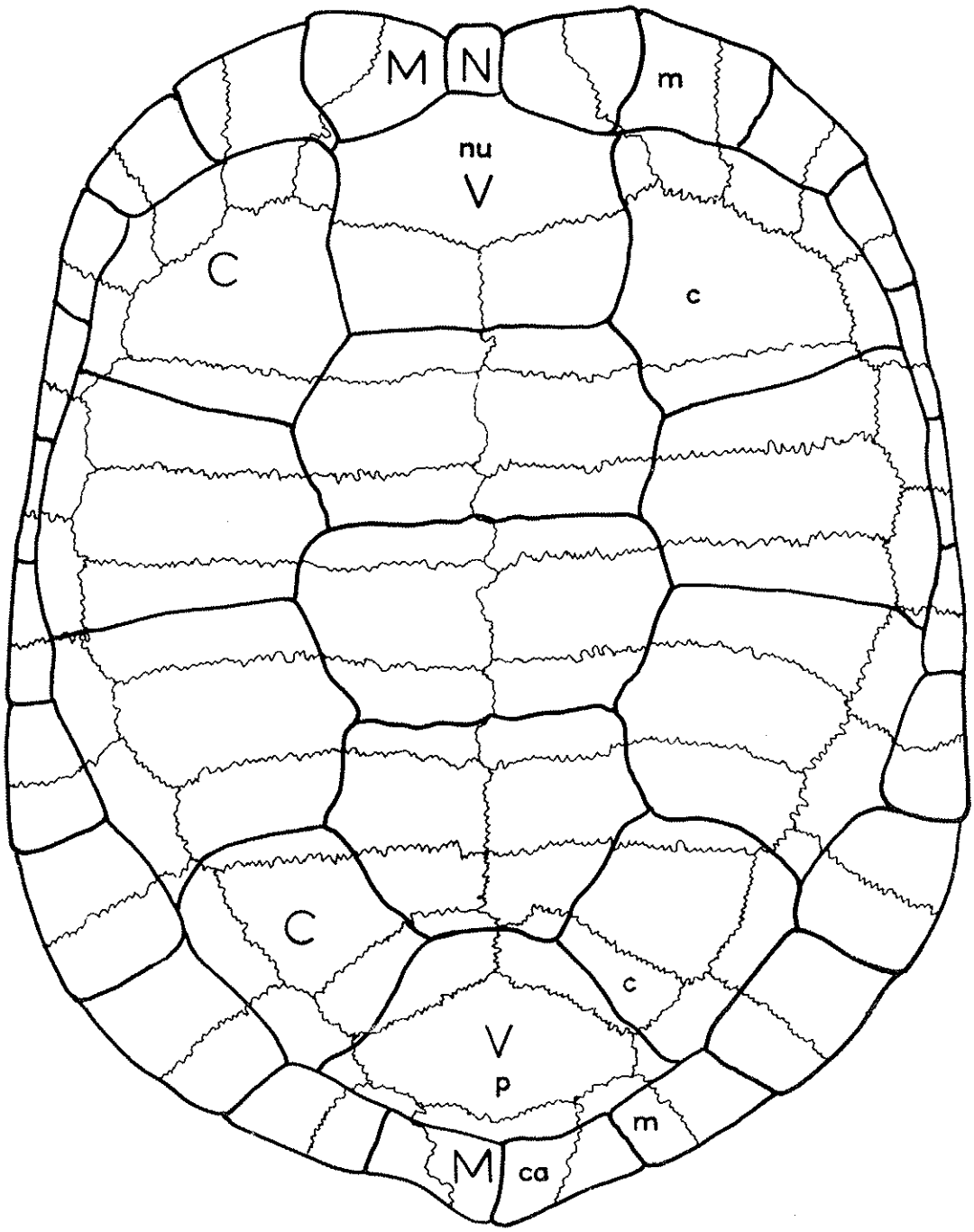


FIGURE 14

P. UMBRINA
PLASTRON

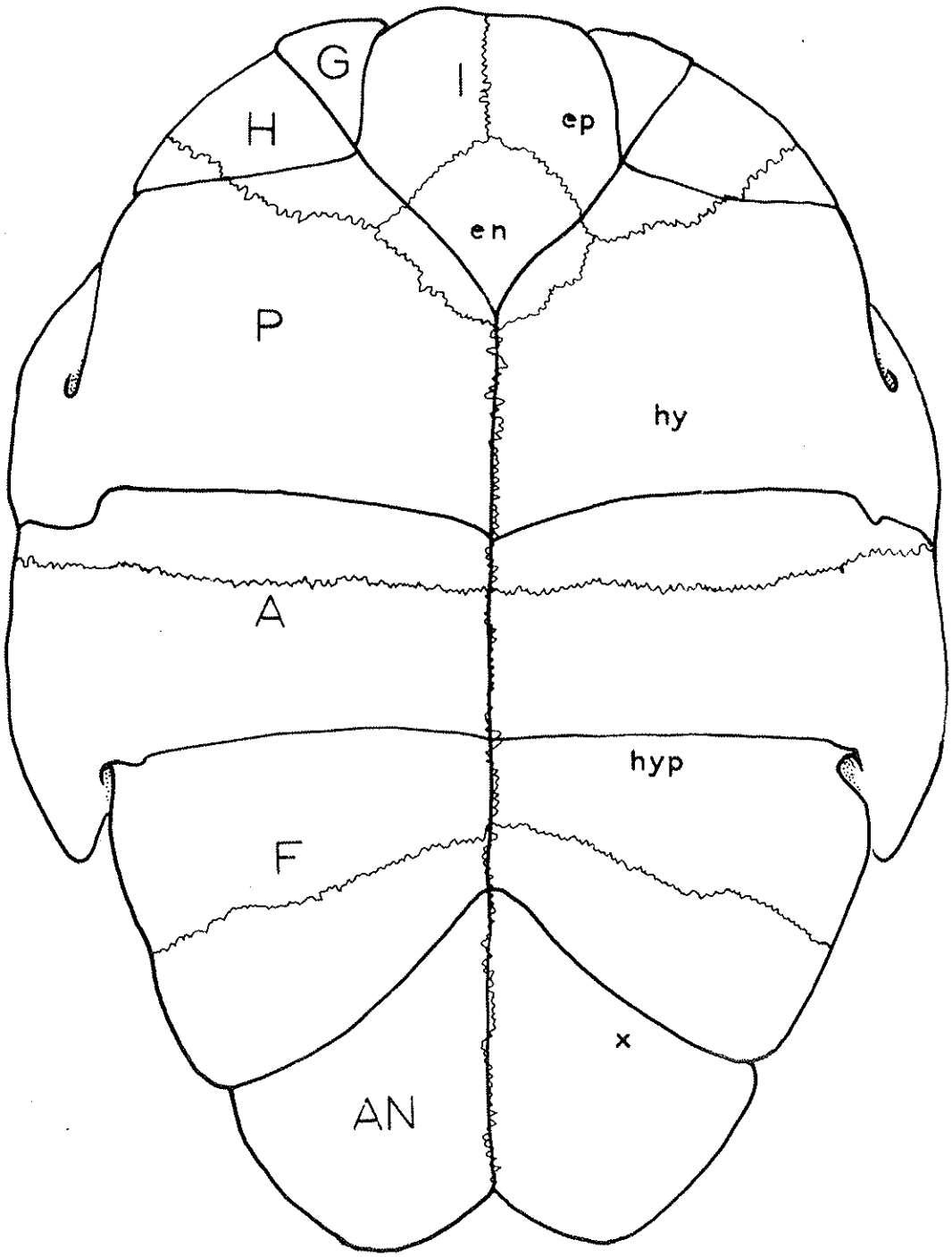


FIGURE 15

C. OBLONGA
CARAPACE

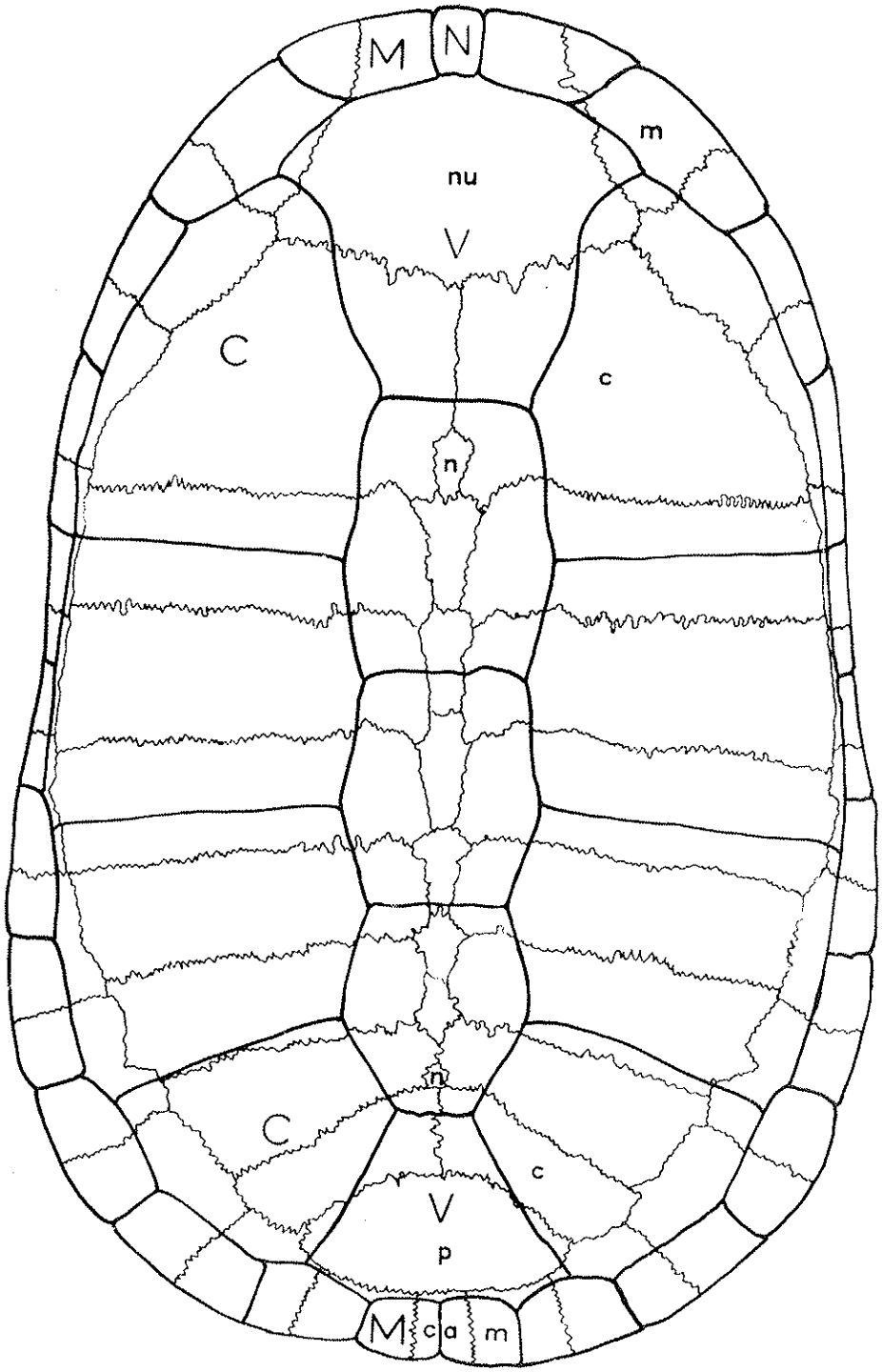


FIGURE 16

C. OBLONGA
PLASTRON

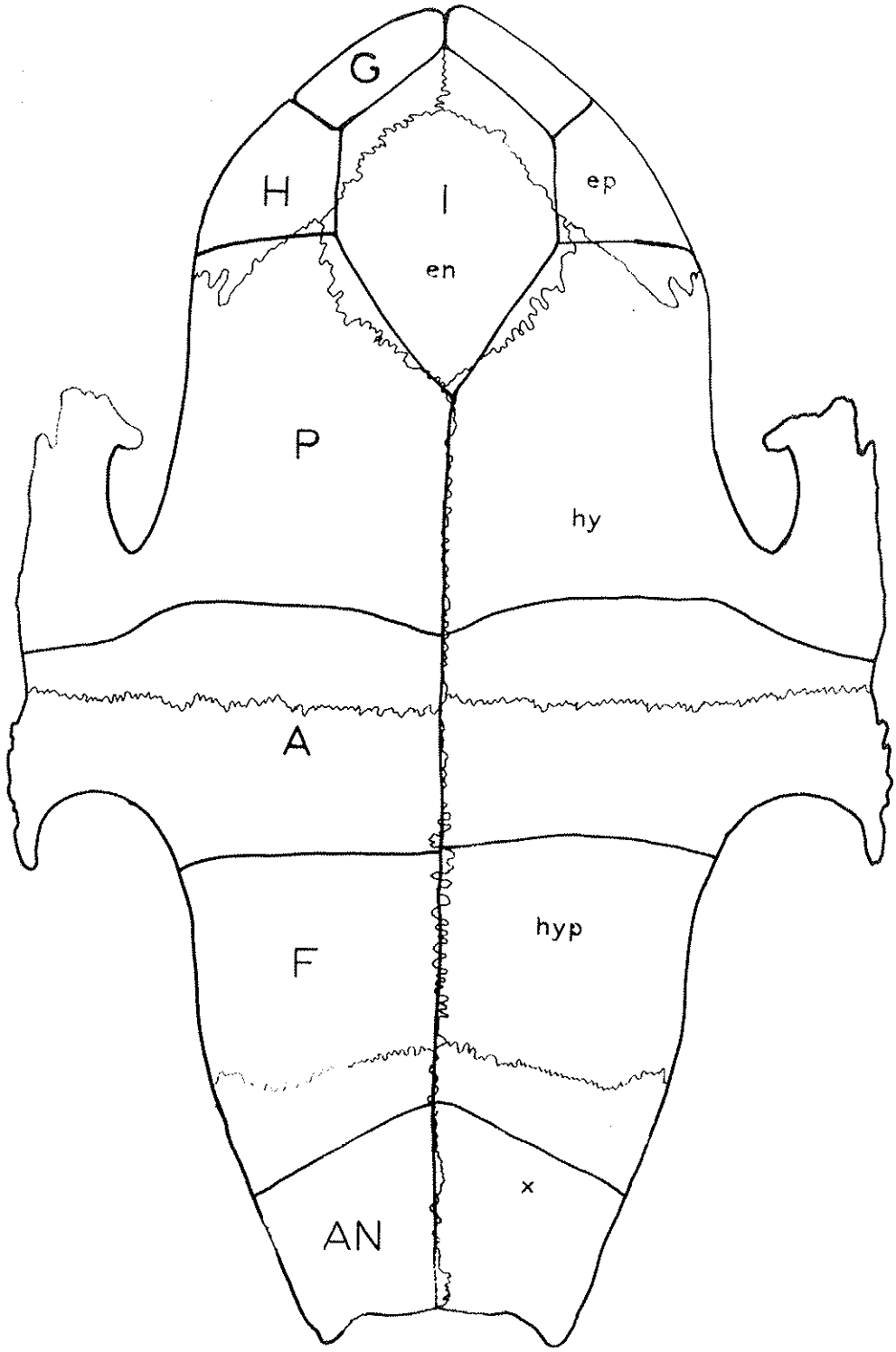


FIGURE 17

P. UMBRINA

SKULL AND MANDIBLE

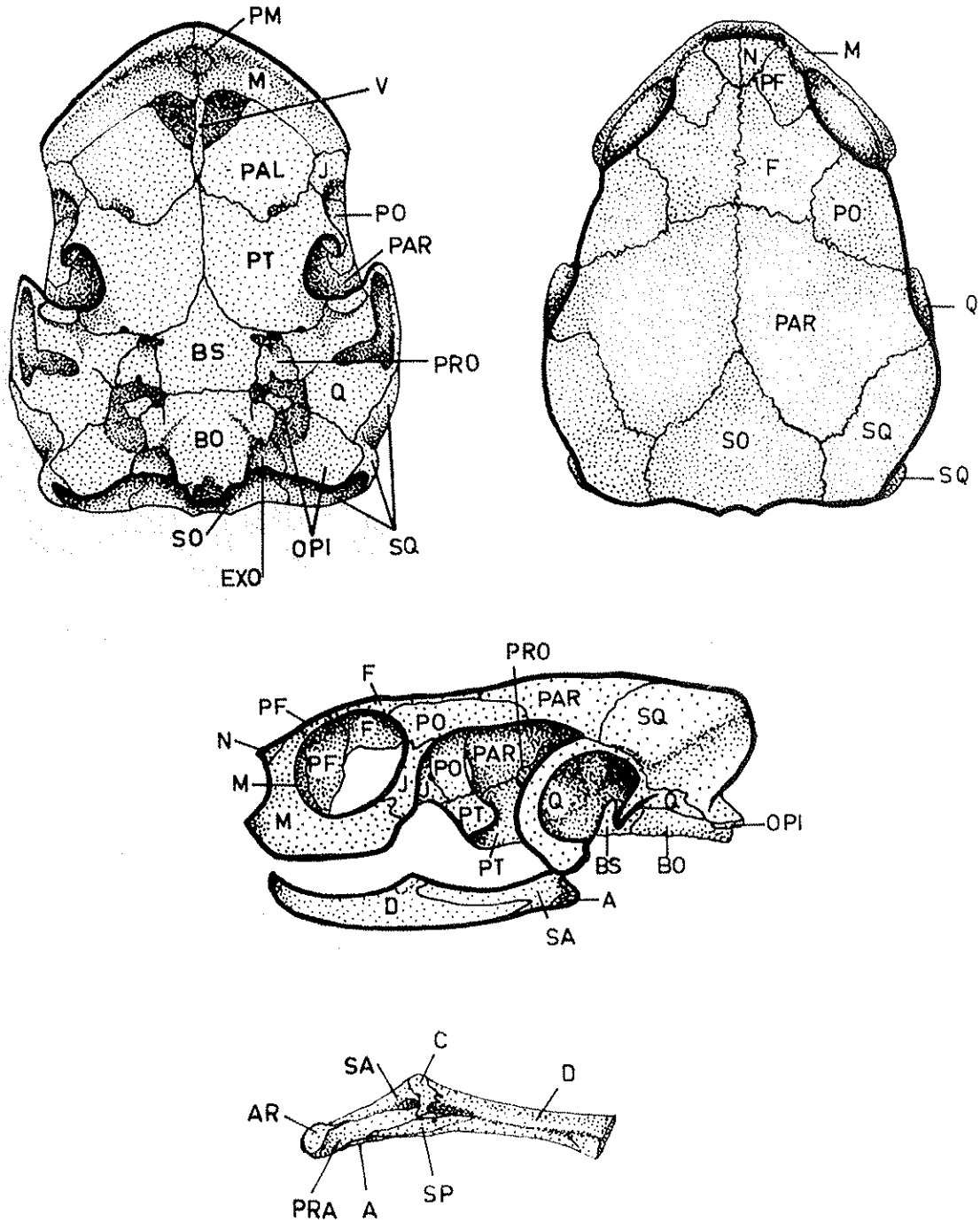


FIGURE 18

EMYDURA MACQUARIA

SKULL AND MANDIBLE

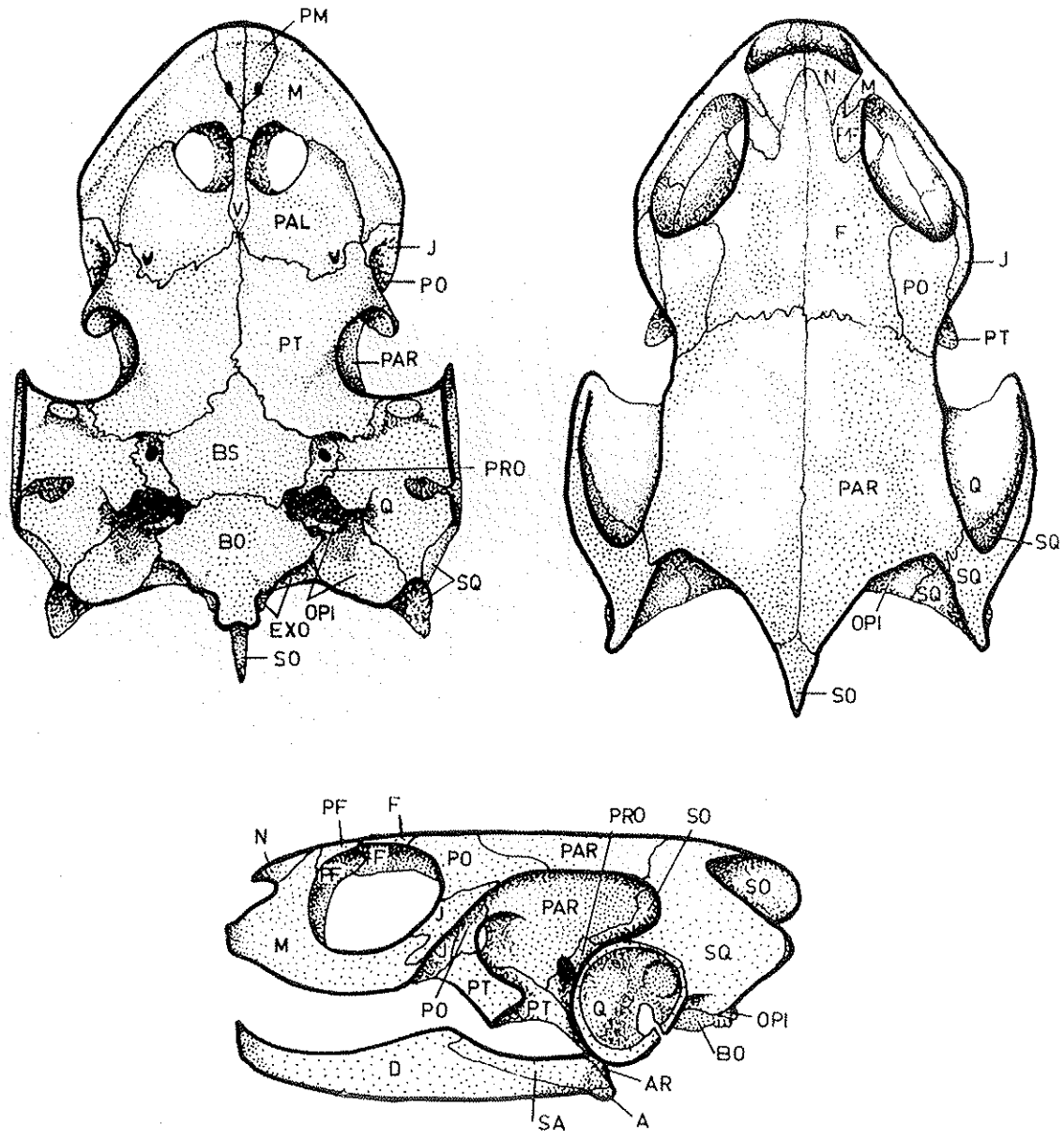


FIGURE 19

ELSEYA LATISTERNUM

SKULL AND MANDIBLE

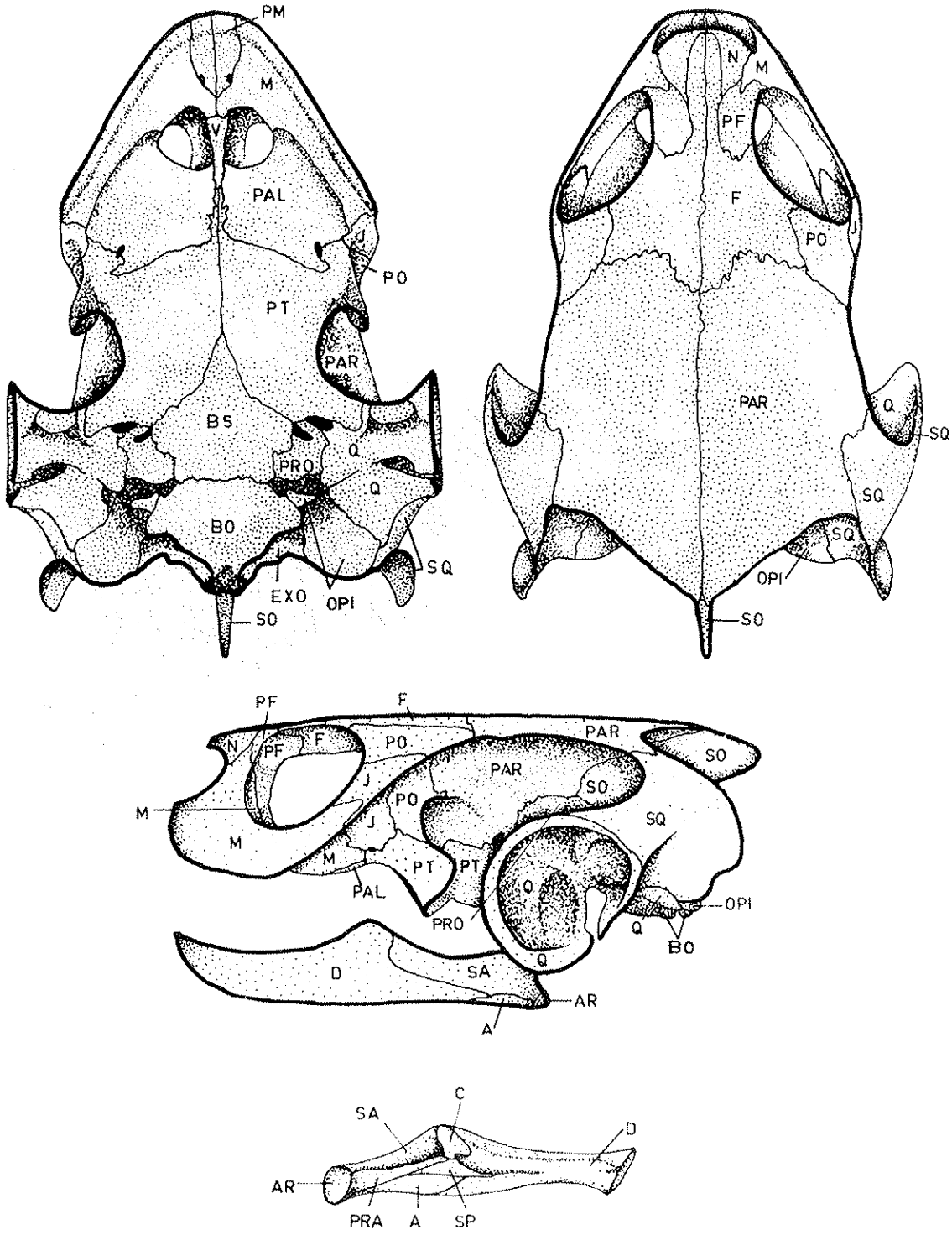


FIGURE 20

CHELODINA OBLONGA
SKULL AND MANDIBLE

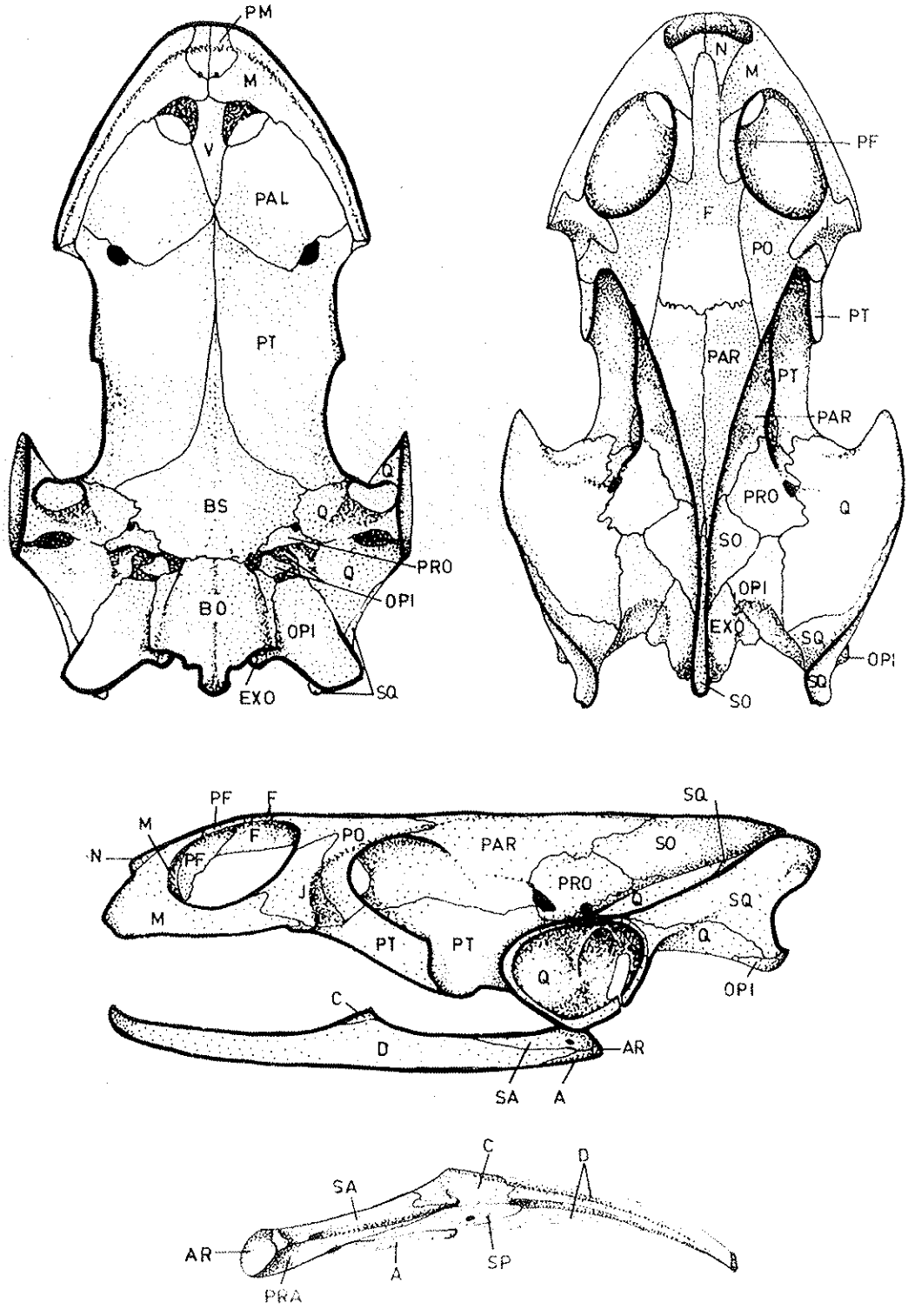


FIGURE 21

THE CLOACAL REGION OF *CHELODINA STEINDACHNERI* DISSECTED FROM THE VENTRAL SURFACE

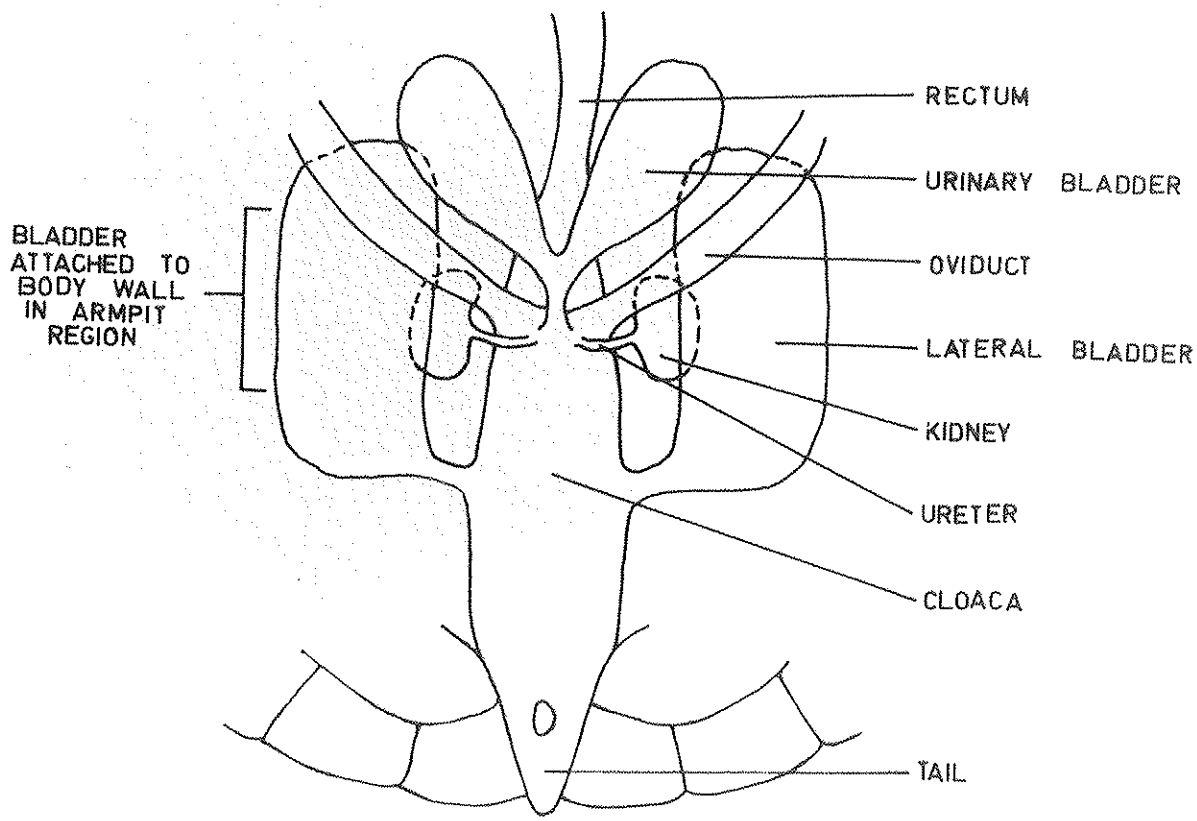


FIGURE 22

DESICCATION RATE
AT 34°C IN DRY AIR

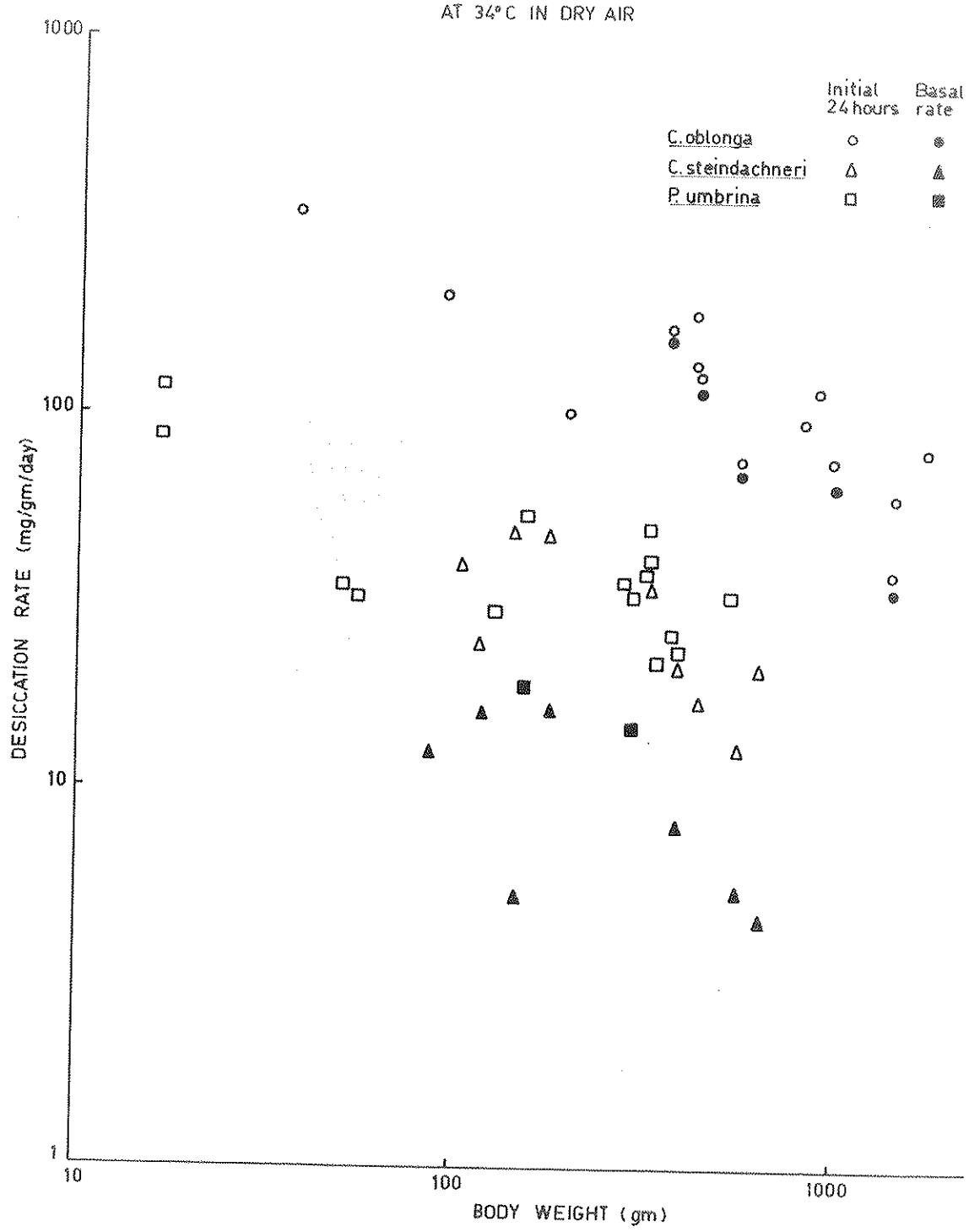


FIGURE 23

CRITICAL THERMAL MAXIMA
(MEAN AND RANGE)

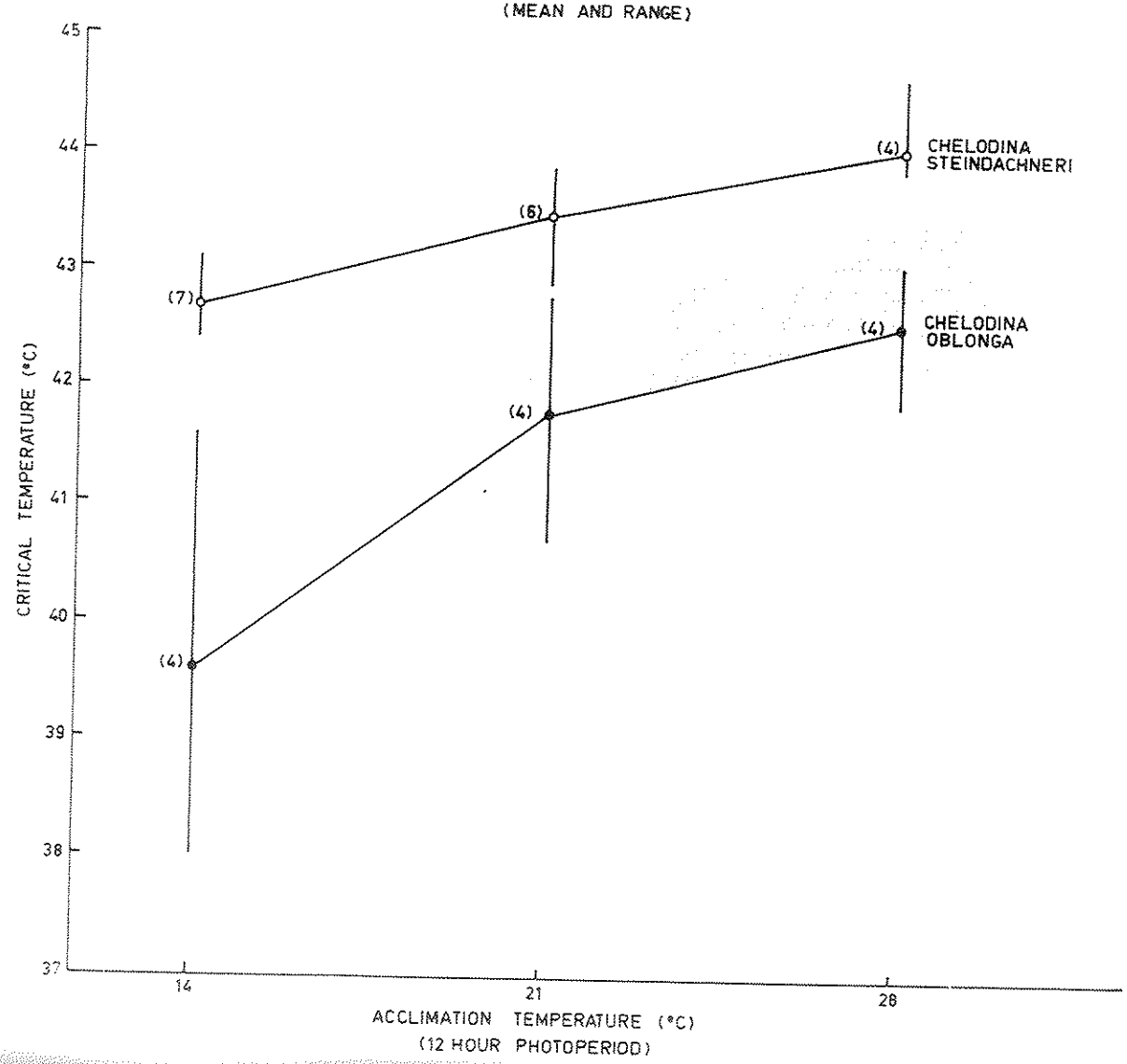


FIGURE 24

BOYDEN CURVES FOR REACTIONS
OF ANTI-CHELODINA OBLONGA

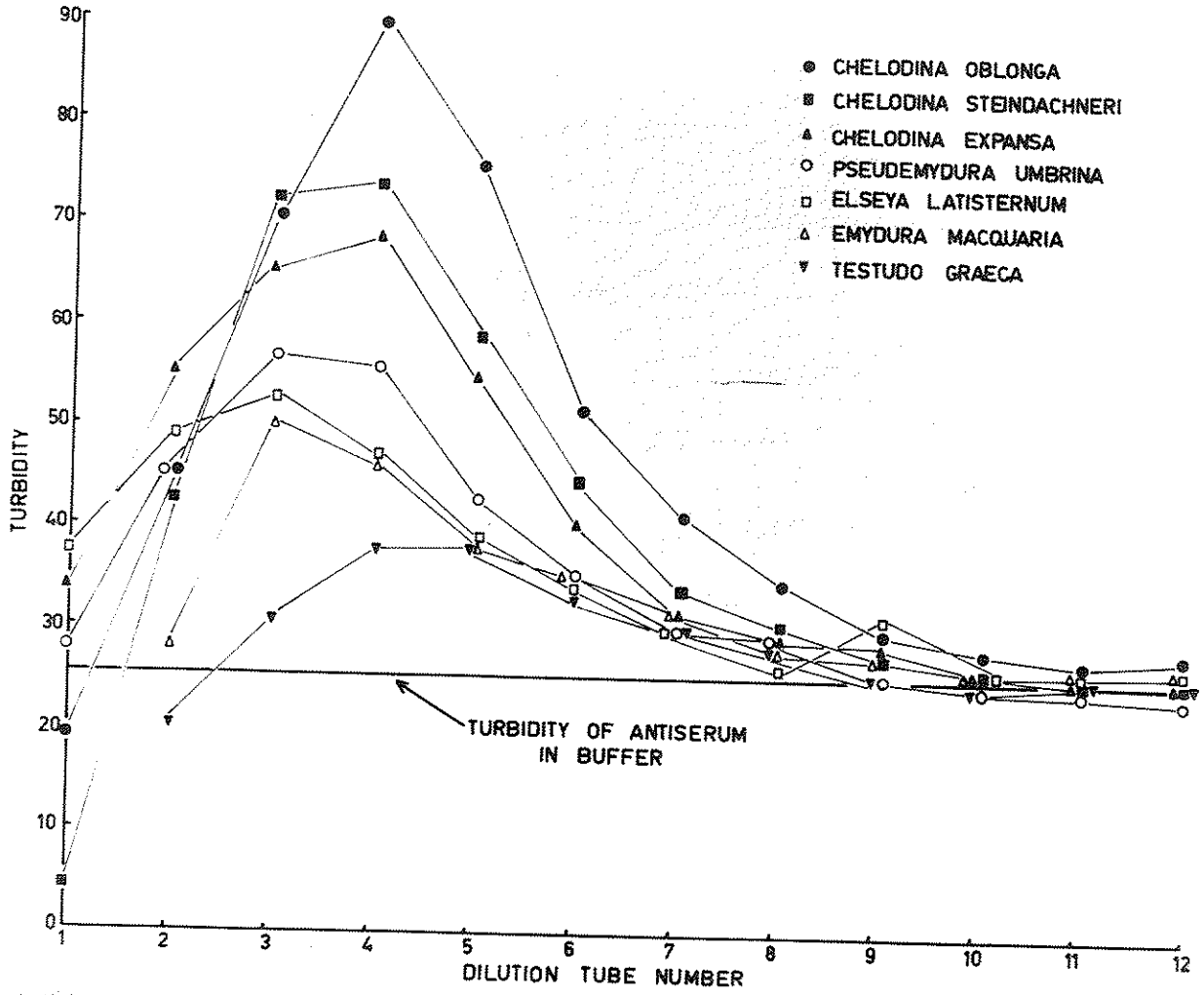


FIGURE 25

IEP REACTIONS OF
ANTI-ELSEYA LATISTERNUM

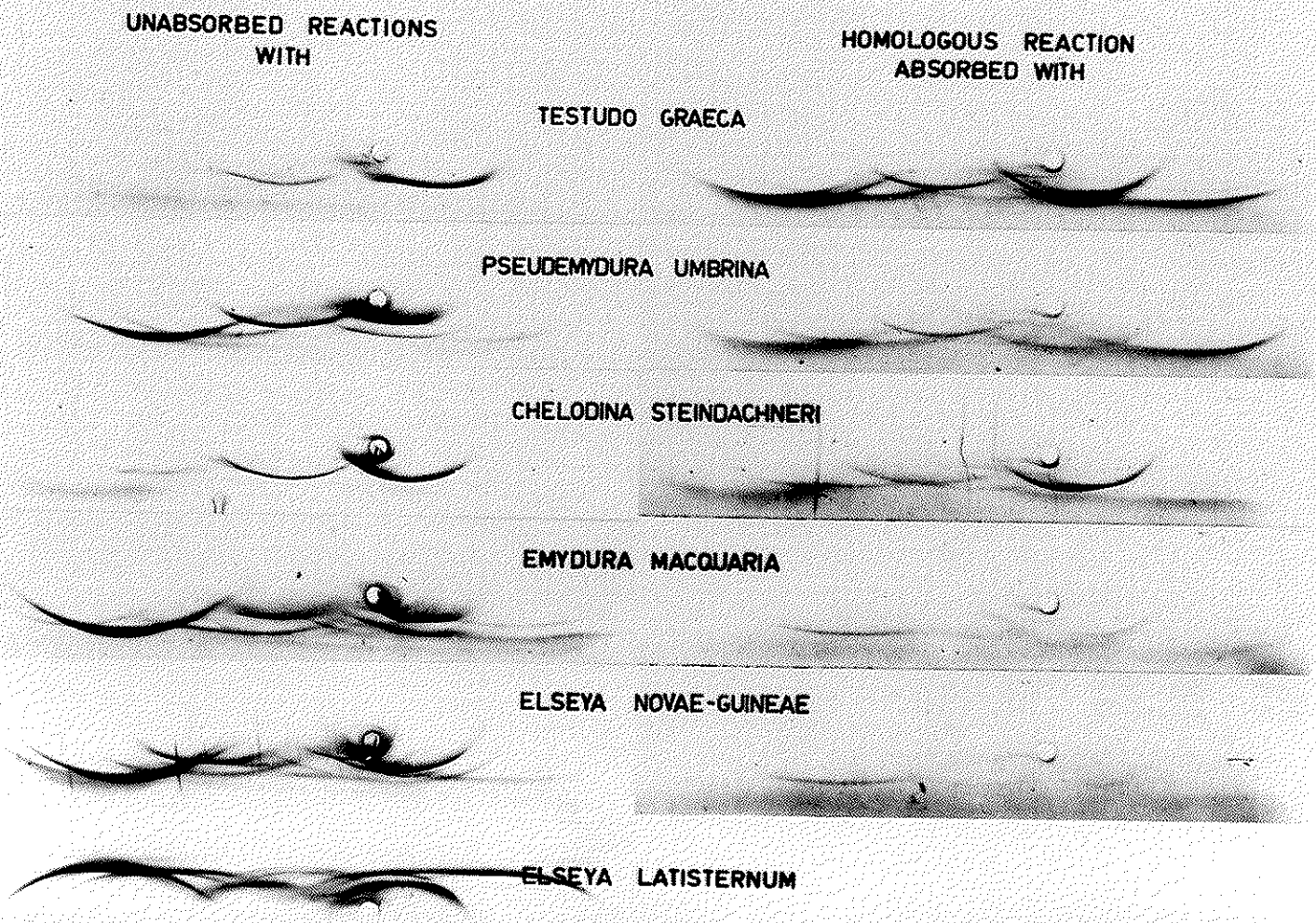


FIGURE 26

DISTRIBUTION OF THE CHELIDAE
IN THE AUSTRALIAN REGION
(SEE TABLE 26)

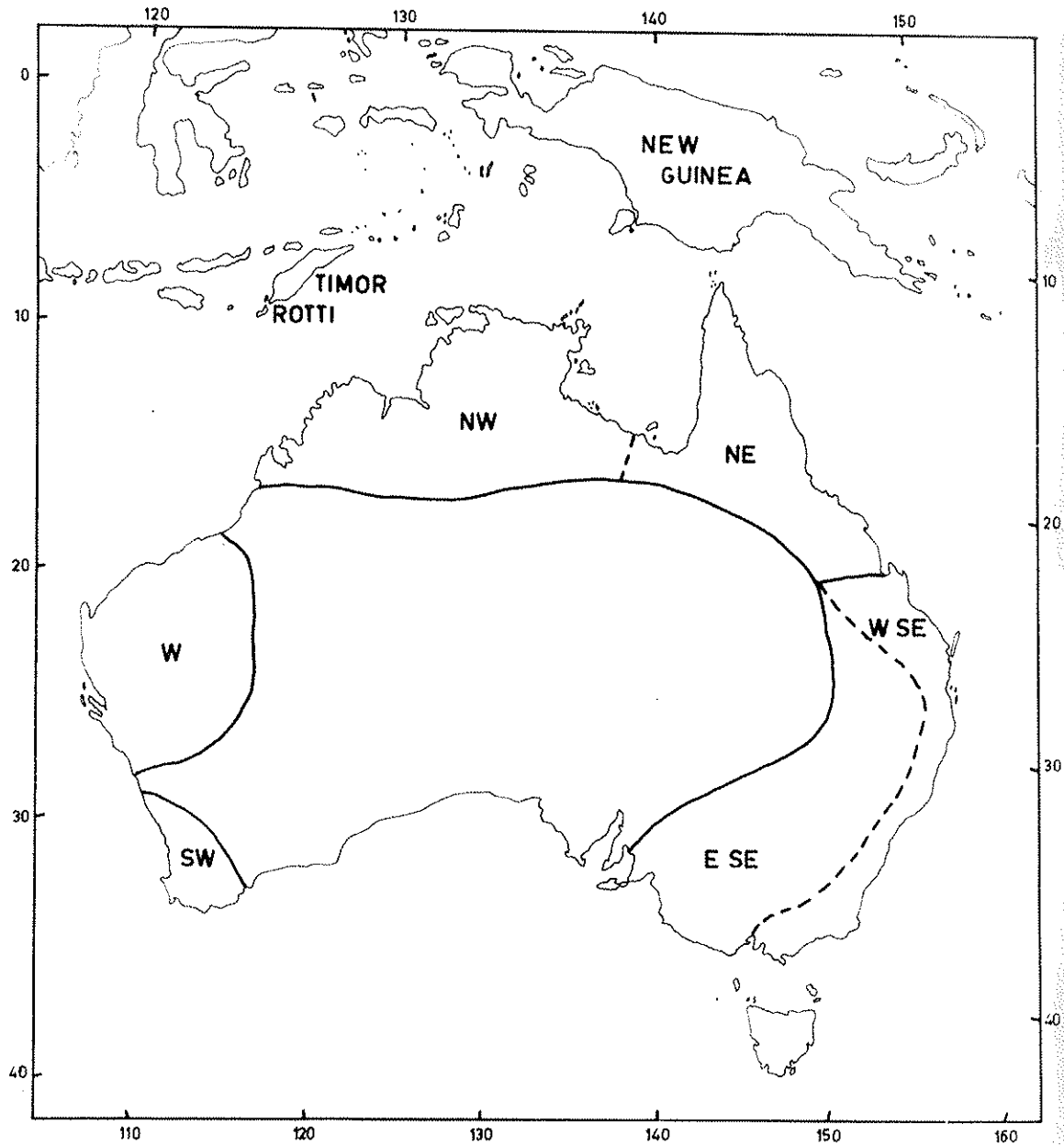


FIGURE 27

AFFINITIES OF THE CHELIDAE
IN AUSTRALIA AND NEW GUINEA

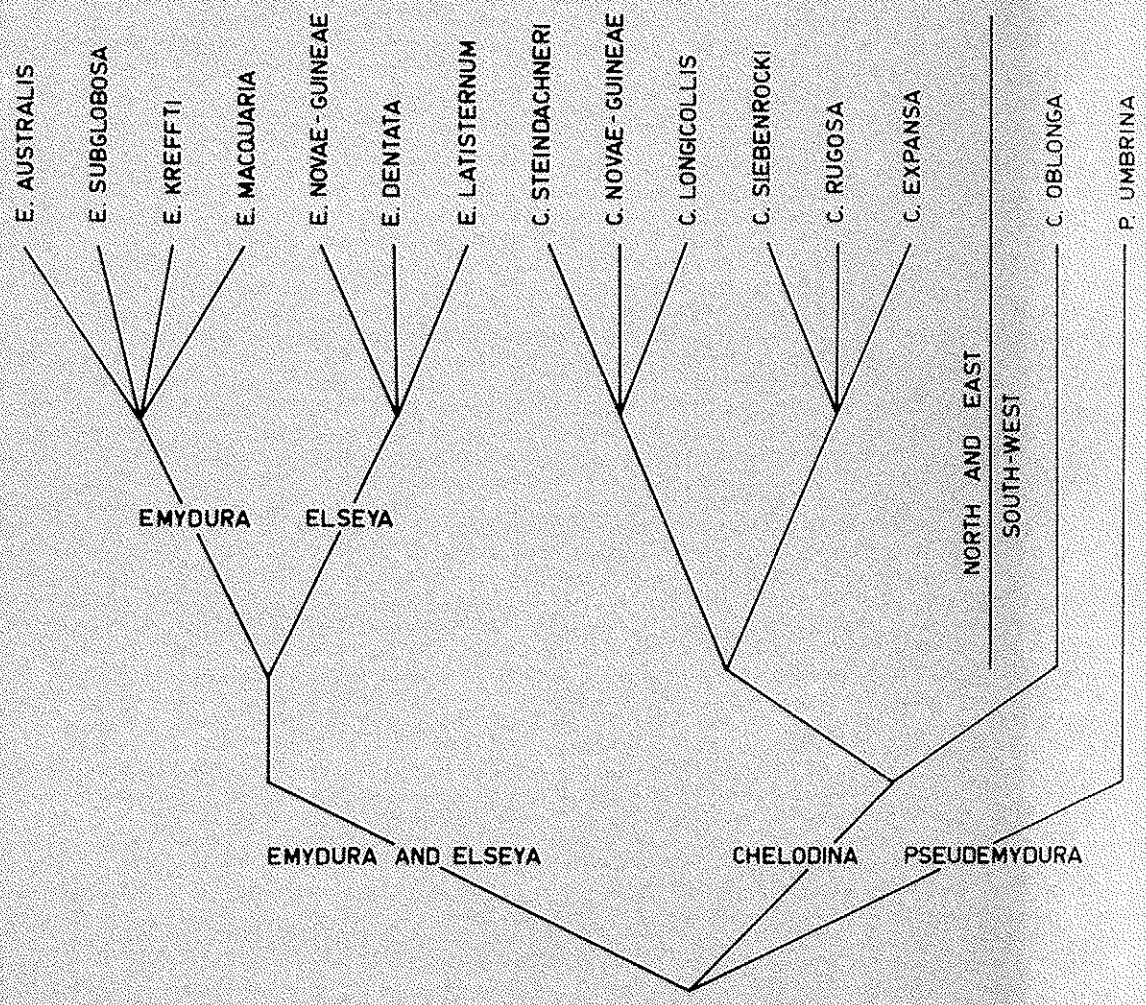


TABLE 1

P. umbrina scute abnormalities

Total No. examined	103	
Typical pattern	26	(25.2%)
Atypical pattern	77	(74.8%)

Splitting

Vertebral two and vertebral three split	41	(39.8%)
Vertebral three split	20	(19.4%)
Vertebral two and vertebral three partly split	2	(1.9%)
Vertebral two partly split	9	(8.7%)
Vertebral three partly split	1	(1.0%)
Vertebral four split	1	(1.0%)
Nuchal split	3	(2.9%)
Nuchal partly split	2	(1.9%)
Total with splitting	73	(70.9%)

Inserts

Between right and left gular and humeral	5	(4.9%)
Between right gular and humeral	4	(3.9%)
Between left gular and humeral	5	(4.9%)
Between vertebrals four and five and right costal four	2	(1.9%)
Between vertebrals four and five and left costal four	2	(1.9%)
Total with inserted scutes	16	(15.5%)

Joined Scutes

Right marginals ten and eleven joined	1	(1.0%)
Only eleven marginals both sides	1	(1.0%)
Total with joined scutes	2	(1.9%)

TABLE 2

Growth rate of *P. umbrina* on the Twin Swamps Reserve calculated for successive years with 6 months standing water.

RING NO.	AGE (Years)	WIDTH FIRST VERTEBRAL SCUTE (mm)	CARAPACE LENGTH (mm)	WEIGHT (gm)
0 (Birth)	0	10.8	29	6
1	$\frac{1}{2}$	19.5	66	50
2	$1\frac{1}{2}$	23.5	84	95
3	$2\frac{1}{2}$	26.0	96	135
4	$3\frac{1}{2}$	28.0	106	175
5	$4\frac{1}{2}$	29.0	114	215
6	$5\frac{1}{2}$	30.0	120	250

TABLE 3

Growth of hatchlings in different years

Twin Swamps Reserve

1966 data - actual
1965 data - 2 actual, 12 calculated from growth rings
1964,63 data - calculated

YEAR HATCHED	RAINFALL (inches)	NO. OF MONTHS OF STANDING WATER	AVERAGE WIDTH FIRST VERTEBRAL SCUTE(RING ONE) (mm)	CARAPACE LENGTH (mm)	WEIGHT (gm)
1966	24.53	3	13.8 (7)	42.3	17.1
1965	34.55	$5\frac{1}{2}$ - 6	18.7 (14)	63.0	45.0
1964	41.84	$6\frac{1}{2}$ - 7	20.2 (20)	70.0	60.0
1963	39.46	6 - $6\frac{1}{2}$?	19.8 (3)	68.0	55.0

TABLE 4

Food

(a)

Stomach Contents

From a ♀ from Twin Swamps Reserve.
Dissected by Dr. W.D.L. Ride, September 7, 1959.
Identified by Dr. D.H. Edward.

					No.
Crustacea	Conchostraca	*Eulimnadia* sp.			71
		Limnetis sp.			5
	Ostracoda	various spp.			18
Insecta	Odonata (Zygoptera)			larvae	4
	Coleoptera	Dytiscidae		larvae	29
				adults	2
	Diptera	Culicidae	Culicinae	larvae	10
			Chaoborinae	larvae	57
				pupae	7

(b)

Faeces (not examined quantitatively) from various tortoises, both reserves partly after Graham (in Lucas, 1963)

Oligochaeta		*Rhododrilus* sp.	
Crustacea	Conchostraca	*Eulimnadia* sp.	
	Ostracada	various spp.	
Insecta	Odonata (Zygoptera)	*Austrolestes analis* plus larvae of other spp.	(larvae)
	(Anisoptera)	*Anax papuensis* plus larvae of other spp.	(larvae)
	Coleoptera	Dytiscidae *Oreodytes* sp. plus other adults and larvae	(adults)
		Hydrophilidae *Hydroporus* sp. plus other adults and larvae	(adults)
Amphibia (Anura)	Hylidae	*Hyla adelaidensis*	(larvae)
	Leptodactylidae	*Neobatrachus pelobatoides*	(larvae)
		Crinia insignifera	(larvae)

TABLE 5

Radio-tracking summary

No.	Date released	Date last observation	No. of observations	No. of days field transmission	Locality	Comments
6♂	6.11.64	15.11.64	2	9	TSR	Animal died
9♀	6.11.64	22. 2.65	16	3 + 66	EBR	Replaced TX 9.11.64, returned 17.12.64, lost 22.2.65
10♂	6.11.64	2.12.65	14	0 + 120 + 22	EBR	First TX failed, recaptured 23.6.65, released 30.6.65, replaced battery 26.10.65, returned 11.11.65, lost 2.12.65
13♀	6.11.64	31.12.65	2	0 + 2	TSR	First TX failed, recaptured 22.12.65, released 29.12.65, lost 31.12.65
16♂	15.11.64	15.11.64	0	0	EBR	TX failed, lost
17♂	20.11.64	8. 1.65	8	58	EBR	TX failed 8.1.65, lost
18♀	20.11.64	8. 3.65	15	0 + 79	EBR	First TX failed, recaptured 5.12.64, released 17.12.64 removed from field 8.3.65
3♀	17.12.64	15. 2.65	12	60	EBR	Lost 15.2.65
20♂	20. 6.65	1.11.66	9	24 + 18	TSR	Lost 14.7.65, recaptured 8.9.66, released 15.10.66 lost 1.11.66
21♂	14. 7.65	11. 5.67	47	121 + 28 + 137 + 142	TSR	Replaced battery 26.10.65, released 11.11.65, lost 2.12.65 recaptured 7.7.66, released 17.7.66, replaced battery 31.11.66 returned 21.12.66, lost 11.5.67, recaptured 22.6.67
25♂	13. 9.65	20. 9.65	1	7	EBR	Lost
26♀	29.12.65	8. 3.67	39	132 + 16 + 138	TSR	Replaced battery 10.5.66, returned 21.5.66, lost 5.6.66 recaptured 15.10.66, released 22.10.66, eaten by fox 8.3.67
40♂	18. 8.66	29. 6.67	46	218 + 89	TSR	Replaced battery 23.3.67, returned 31.3.67, TX removed 29.6.67
46♂	22. 9.66	16. 6.67	31	184 + 88	TSR	Replaced battery 23.3.67, returned 31.3.67, TX removed 16.6.67
57♂	22. 9.66	16. 6.67	22	14 + 96 + 118	TSR	Replaced TX 6.10.66, returned 19.10.66, replaced battery 10.2.67, returned 1.3.67, TX removed 16.6.67
33♀	15.10.66	29. 6.67	33	186 + 64	TSR	Replaced battery 18.4.67, returned 27.4.67, TX removed 29.6.67
31♂	15.10.66	29. 6.67	35	186 + 64	TSR	Replaced battery 18.4.67, returned 27.4.67, TX removed 29.6.67
56♀	19.10.66	22. 6.67	31	156 + 83	TSR	Replaced battery 23.3.67, returned 31.3.67, TX removed 22.6.67
45♂	22.10.66	22.10.66	0	0	TSR	Lost
86♂	28.10.66	8. 6.67	2	224	TSR	Receiver crystal malfunction, lost for most of the time
67♀	28.10.66	22. 6.67	28	173 + 67	TSR	Replaced battery 18.4.67, returned 27.4.67, TX removed 22.6.67
TOTALS			393	2292		

TX transmitter EBR Ellen Brook Reserve TSR Twin Swamps Reserve

TABLE 6

Summer temperature records
(°C, mean and range)

Location	Dates	Aestivation Site		Surface		Air		Official Air Swan Research Station	
		Maximum	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum	Minimum
Ellen Brook in tunnel	1. 2.66 -28. 2.66	28.2 (25.0-31.5)	21.8 (18.0-26.0)	40.6 (30.0-54.0)	13.2 (6.5-27.0)	-	-	31.9 (24.0-42.0)	16.2 (8.5-24.0)
Twin Swamps under *Banksia* & *Acacia* litter	11. 2.66 - 4. 3.66	26.7 (19.5-33.5)	17.0 (11.5-23.5)	-	-	34.5 (24.5-47.0)	12.7 (2.5-24.0)	31.4 (24.0-42.0)	14.8 (8.5-24.0)
Twin Swamps under *E.Todtiana* branch	22.12.66 -29.12.66	25.8 (20.0-29.5)	16.3 (14.0-19.5)	45.9 (38.0-55.0)	7.8 (3.0-15.0)	37.4 (30.0-45.0)	8.2 (3.0-16.0)	26.3 (24.0-30.5)	11.9 (7.0-15.5)
Twin Swamps deepish tunnel in sand	22.12.66 - 4. 1.67	23.0 (19.5-25.5)	20.0 (17.0-22.5)	59.5 (40.0-68.0)	9.0 (3.5-14.0)	39.4 (30.0-49.5)	9.4 (4.0-16.0)	29.5 (24.0-36.5)	12.5 (7.0-15.5)
Twin Swamps shallow tunnel in sand	25. 1.67 - 7. 3.67	30.9 (28.0-34.0)	25.5 (21.0-29.0)	60.1 (46.5-70.0)	13.3 (4.5-22.5)	40.1 (30.0-48.5)	14.8 (4.0-24.5)	35.1 (26.5-43.0)	18.8 (9.5-27.0)
Twin Swamps under *Banksia* litter	22. 2.67 - 3. 3.67	29.4 (24.5-31.5)	17.5 (13.0-22.5)	42.7 (37.5-45.5)	15.4 (8.0-21.5)	37.9 (30.0-42.0)	15.7 (7.5-23.0)	34.6 (27.0-37.0)	16.6 (11.0-23.0)

TABLE 7

Rates of water loss, 34°C, dry air. Surface areas calculated using Benedict's (1932) formula.

Species	Initial 24 hours		Final steady rate	
	No.	Rate ($mg/cm^2/day$)	No.	Rate ($mg/cm^2/day$)
Chelodina oblonga	14	86.8 (42.3 - 136.2)	5	72.7 (36.6 - 118.8)
Chelodina steindachneri	11	23.9 (10.5 - 44.3)	5	5.6 (2.7 - 9.2)
Pseudemydura umbrina	15	21.2 (11.7 - 34.8)	2	10.1 (9.8 - 10.4)

TABLE 8

Cutaneous and repiratory water loss of *C. oblonga* and *C. steindachneri*.

34 °C, dry air.

Species	Body weight (gm)	Initial 24 hours ($mg/cm^2/day$)		Basal rate ($mg/cm^2/day$)	
		cutaneous	respiratory	cutaneous	respiratory
C. oblonga	584	72.1	5.4	72.0	4.0
	882	91.5	8.3	76.0	6.6
	854	83.1	6.9	64.3	5.8
	mean	85.5 (92.5%)	6.9 (7.5%)	70.8 (92.8%)	5.5 (7.2%)
C. steindachneri	558	14.2	4.1	2.3	1.5
	320	15.2	8.7	6.1	3.1
	178	18.8	7.8	6.4	2.8
	mean	16.1 (70.0%)	6.9 (30.0%)	4.9 (66.2%)	2.5 (33.8%)

TABLE 9

Comparative rates of water loss.

Initial 24 hours, 34°C, dry air. Surface area calculated using Benedict's (1932) formula.

Species	No. tested	Rate ($mg/cm^2/day$)
Chelodina expansa	1	104.1
Chelodina oblonga	14	86.8 (42.3 - 136.2)
Chelodina ?rugosa	1	73.2
Elseya latisternum	1	72.8
Emydura macquaria	1	71.4
Elseya dentata	1	57.0
Chelodina longicollis	5	37.7 (20.5 - 73.6)
Emydura kreffti	1	32.6
Chelodina novae-guineae	1	28.4
Chelodina steindachneri	11	23.9 (10.5 - 44.3)
Pseudemydura umbrina	15	21.2 (11.7 - 34.9)
Clemmys caspica leprosa	1	34.0
Testudo graeca	1	5.4

TABLE 10

Heart rates of C. oblonga and C. steindachneri after 24 hours at 20°C, immediately after heating to 35°C and after three days at 35°C.

Species		Body weight (gm)	Heart rate (beats/min)		
			basal 20°C	initial 35°C	basal 35°C
C. oblonga	1	550	5.5	70.6	65.0
	2	740	6.0	53.5	26.2
	3	986	6.3	39.0	20.5
C. steindachneri	1	375	4.0	55.4	22.0
	2	380	4.2	52.6	23.5
	3	780	4.0	32.3	14.8

TABLE 11

CO_2 production of *C. oblonga* and *C. steindachneri* immediately after heating to 35°C, after 24 hours and after three days.

Species		Body weight (gm)	CO_2 production (mg/gm/hour)		
			initial	24 hours	3 days
C. oblonga		851	0.088	0.063	0.048
C. steindachneri	1	343	0.075	0.062	0.059
	2	348	0.111	0.084	0.071

TABLE 12

Lethal Dehydration

Species		Body weight (gm)	% body weight lost at death	% total body water lost at death
C. oblonga	1	38	32.1	39.5
	2	363	31.9	42.9
	3	438	32.0	39.3
	4	557	31.3	42.6
	5	1401	31.0	41.6
C. steindachneri	1	87	40.3	50.6
	2	145	37.1	50.3

TABLE 13

Water conservation experiment

Species	Initial weight (gm)	% body weight lost when killed	% body weight lost per day	Total body water (%)	% TBW lost when killed
C. oblonga	726.6 (386 - 938)	28.1 (19.1 - 31.7)	20°C (4) 1.22 (1.18 -- 1.27)	77.2 (71.1 - 81.1)	37.4 (23.5 - 42.6)
			30°C (7) 2.74 (2.06 - 3.65)		
C. steindachneri	241.4 (109 - 465)	27.2 (24.8 - 30.1)	20°C (1) 0.22	77.5 (67.8 - 80.7)	37.2 (30.6 - 42.3)
			30°C (4) 0.28 (0.24 - 0.32)		

TABLE 14

Water conservation experiment

Electrolytes

	Plasma			Urine		
	Haematocrit (%)	Na^+	K^+	Volume (ml)	Na^+	K^+
C. oblonga (hydrated) (5)	18.2 (6.3 - 29.5)	136 (126 - 148)	2.5 (1.1 - 3.5)	35.6 (5.0 - 61.0)	5.4 (0.0 - 13.0)	1.0 (0.2 - 2.1)
C. oblonga (dehydrated) (11)	21.3 (12.4 - 28.4)	220 (179 - 252)	4.2 (3.2 - 6.0)	3.4 (1.0 - 6.5)	5.5 (1.0 - 33.0)	69.0 (21.5 - 104)
C. steindachneri (hydrated) (4)	17.6 (11.1 - 22.9)	152 (141 - 172)	3.7 (2.3 - 5.9)	8.9 (6.5 - 12.5)	5.7 (2.0 - 8.0)	0.4 (0.2 - 0.5)
C. steindachneri (dehydrated) (5)	21.9 (16.7 - 25.1)	165 (150 - 183)	2.9 (1.9 - 3.8)	2.3 (1.0 - 5.0)	8.6 (3.6 - 19.3)	145.9 (123 - 180)

TABLE 15

Osmolality and urea concentration of the urine and plasma of some C. oblonga and C. steindachneri.

Species	Animal No.	Plasma		Urine	
		Osmolality (milliosmoles)	Urea (mg/100 ml)	Osmolality (milliosmoles)	Urea (mg/100 ml)
C. oblonga hydrated	71	258	13.2	59	52.1
	72	-	14.7	-	35.3
C. oblonga dehydrated	62	422	139.8	390	155.0
	64	-	232.5	-	262.5
C. steindachneri hydrated	28	-	9.6	-	24.7
	47	274	4.8	32	14.4
C. steindachneri dehydrated	41	417	483.0	393	594.0
	46	436	280.0	396	271.0

TABLE 16

Water conservation experiment
Analysis of bladder fluids
(mg N / 100 ml)

SPECIES	VOLUME (ml)	AMMONIA	%	UREA	%	URATES	%
C. oblonga hydrated (5)	35.6 (5.0-61.0)	18.8 (5.2-32.9)	44.5	19.9 (10.5-33.5)	47.0	3.7 (1.6-6.3)	8.5
C. oblonga dehydrated (11)	3.4 (1.0-6.5)	164.3 (80.6-231.0)	24.6	130.4 (53.0-172.2)	19.6	372.5 (49.4-1085)	55.8
C. steindachneri hydrated (4)	8.9 (6.5-12.5)	2.8 (2.6-3.1)	23.2	5.4 (0.2-11.5)	44.6	3.9 (2.9-5.4)	32.2
C. steindachneri dehydrated (5)	2.3 (1.0-5.0)	3.8 (0.2-9.5)	0.5	164.0 (82.1-276.8)	19.6	669.6 (358-1612)	79.9

TABLE 17

IEP reactions of absorbed anti-2 (*Elseya latisternum*)

Absorbent	Sera tested															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	1	5	3	3	3	3	3	3	1	1	1	1	2	2	2	1
3	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	5	2	1	0	0	1	1	0	0	1	0	0	1	1	0
8	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	2	5	3	3	3	3	3	3	0	0	0	0	0	0	0	0
12	0	5	3	3	3	3	3	3	0	0	0	0	0	0	0	0
16	2	5	3	3	3	3	3	3	2	2	2	2	2	2	2	0

Note: Absorption with 1 is incomplete.

TABLE 18

IEP reactions of absorbed anti-5 (Emydura macquaria)

Absorbent	Sera tested															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	0	2	2	2	5	4	4	4	0	0	0	0	0	0	0	0
2	0	0	0	2	5	5	5	4	0	0	0	0	0	0	0	0
3	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	2	3	4	3	5	5	4	5	0	1	1	1	1	1	1	0
12	0	3	3	3	5	4	4	4	0	0	0	0	0	1	0	0
16	3	4	4	3	5	5	4	4	2	2	2	2	2	2	2	0

TABLE 19

IEP reactions of absorbed anti-12 (*Chelodina oblonga*)

Absorbent	Sera tested															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	0	0	0	0	1	1	2	1	3	4	3	5	4	4	4	0
2	1	0	1	0	0	0	0	1	4	4	3	5	4	4	4	0
3	0	0	0	0	0	0	0	0	4	5	3	5	4	4	4	0
5	1	1	1	1	0	1	1	1	4	4	3	5	4	4	3	0
9	0	0	1	0	0	0	0	0	0	2	2	5	2	2	2	0
13	0	0	0	0	0	0	0	0	1	3	2	5	0	2	3	0
16	2	2	2	2	2	2	2	2	4	4	4	5	4	4	4	0

Table 20: Probabilities of association of 16 sera, computed by Goodall's (1966) method, using the data of Tables 12-14. Probabilities are given in E-form.

Sera	Sera 1	2	3	4	5	6	7	8
1	0.000E+00	0.446E+00	0.960E-01	0.343E+00	0.419E+00	0.220E+00	0.605E+00	0.223E+00
2	0.446E+00	0.000E+00	0.349E-01	0.112E-01	0.440E+00	0.542E+00	0.390E+00	0.484E+00
3	0.960E-01	0.349E-01	0.000E+00	0.451E-03	0.984E-01	0.304E-01	0.192E-02	0.133E-02
4	0.343E+00	0.112E-01	0.451E-03	0.000E+00	0.654E-01	0.189E-01	0.417E-02	0.692E-02
5	0.419E+00	0.440E+00	0.984E-01	0.654E-01	0.000E+00	0.196E-04	0.258E-02	0.364E-02
6	0.220E+00	0.542E+00	0.304E-01	0.189E-01	0.196E-04	0.000E+00	0.326E-04	0.490E-04
7	0.605E+00	0.390E+00	0.192E-02	0.417E-02	0.258E-02	0.326E-04	0.000E+00	0.498E-04
8	0.223E+00	0.484E+00	0.133E-02	0.692E-02	0.364E-02	0.490E-04	0.498E-04	0.000E+00
9	0.355E+00	0.947E+00	0.983E+00	0.981E+00	0.999E+00	0.994E+00	0.985E+00	0.991E+00
10	0.786E+00	0.983E+00	0.991E+00	0.998E+00	0.999E+00	0.999E+00	0.999E+00	0.999E+00
11	0.737E+00	0.793E+00	0.954E+00	0.946E+00	0.999E+00	0.998E+00	0.954E+00	0.973E+00
12	0.879E+00	0.996E+00	0.999E+00	0.999E+00	0.100E+01	0.999E+00	0.999E+00	0.999E+00
13	0.721E+00	0.980E+00	0.945E+00	0.979E+00	0.999E+00	0.994E+00	0.993E+00	0.992E+00
14	0.826E+00	0.837E+00	0.960E+00	0.959E+00	0.999E+00	0.999E+00	0.984E+00	0.982E+00
15	0.881E+00	0.975E+00	0.971E+00	0.971E+00	0.999E+00	0.999E+00	0.989E+00	0.988E+00
16	0.902E-01	0.312E-02	0.735E+00	0.627E+00	0.694E+00	0.834E+00	0.879E+00	0.900E+00

Sera	9	10	11	12	13	14	15	16
1	0.355E+00	0.786E+00	0.737E+00	0.879E+00	0.721E+00	0.826E+00	0.881E+00	0.902E-01
2	0.947E+00	0.983E+00	0.793E+00	0.996E+00	0.980E+00	0.837E+00	0.975E+00	0.312E-02
3	0.983E+00	0.991E+00	0.954E+00	0.999E+00	0.945E+00	0.960E+00	0.971E+00	0.735E+00
4	0.981E+00	0.998E+00	0.946E+00	0.999E+00	0.979E+00	0.959E+00	0.971E+00	0.627E+00
5	0.999E+00	0.999E+00	0.999E+00	0.100E+01	0.999E+00	0.999E+00	0.999E+00	0.694E+00
6	0.994E+00	0.999E+00	0.998E+00	0.999E+00	0.994E+00	0.999E+00	0.999E+00	0.834E+00
7	0.985E+00	0.999E+00	0.954E+00	0.999E+00	0.993E+00	0.984E+00	0.989E+00	0.879E+00
8	0.991E+00	0.999E+00	0.973E+00	0.999E+00	0.992E+00	0.982E+00	0.988E+00	0.900E+00
9	0.000E+00	0.132E-01	0.851E-02	0.157E+00	0.626E-02	0.130E-01	0.192E-01	0.320E+00
10	0.132E-01	0.000E+00	0.118E-01	0.706E-02	0.182E-02	0.306E-02	0.284E-03	0.751E+00
11	0.851E-02	0.118E-01	0.000E+00	0.223E+00	0.201E-01	0.215E-02	0.518E-03	0.681E+00
12	0.157E+00	0.706E-02	0.223E+00	0.000E+00	0.126E+00	0.208E+00	0.161E+00	0.826E+00
13	0.626E-02	0.182E-02	0.201E-01	0.126E+00	0.000E+00	0.178E-03	0.277E-03	0.683E+00
14	0.130E-01	0.306E-02	0.215E-02	0.208E+00	0.178E-03	0.000E+00	0.464E-04	0.922E+00
15	0.192E-01	0.284E-03	0.518E-03	0.161E+00	0.277E-03	0.464E-04	0.000E+00	0.847E+00
16	0.320E+00	0.751E+00	0.681E+00	0.826E+00	0.683E+00	0.922E+00	0.847E+00	0.000E+00

Table 21: Probabilities of association of 12 sera, computed by Goodall's (1966) method, after removal of data (from Tables 12-14) on sera 5-8. Probabilities are given in E-form.

Sera	Sera 1	2	3	4	9	10
1	0.000E+00	0.536E+00	0.489E-01	0.155E+00	0.506E+00	0.967E+00
2	0.536E+00	0.000E+00	0.653E-02	0.213E-02	0.914E+00	0.988E+00
3	0.489E-01	0.653E-02	0.000E+00	0.566E-06	0.993E+00	0.999E+00
4	0.155E+00	0.213E-02	0.566E-06	0.000E+00	0.990E+00	0.999E+00
9	0.506E+00	0.914E+00	0.993E+00	0.990E+00	0.000E+00	0.658E-01
10	0.967E+00	0.988E+00	0.999E+00	0.999E+00	0.658E-01	0.000E+00
11	0.908E+00	0.824E+00	0.979E+00	0.971E+00	0.229E-01	0.594E-01
12	0.991E+00	0.999E+00	0.999E+00	0.999E+00	0.255E+00	0.194E-01
13	0.909E+00	0.982E+00	0.974E+00	0.992E+00	0.367E-01	0.145E-01
14	0.971E+00	0.875E+00	0.981E+00	0.976E+00	0.566E-01	0.184E-01
15	0.982E+00	0.973E+00	0.987E+00	0.983E+00	0.812E-01	0.265E-02
16	0.138E+00	0.349E-02	0.700E+00	0.450E+00	0.346E+00	0.898E+00

Sera	11	12	13	14	15	16
1	0.908E+00	0.991E+00	0.909E+00	0.971E+00	0.982E+00	0.138E+00
2	0.824E+00	0.999E+00	0.982E+00	0.875E+00	0.973E+00	0.349E-02
3	0.979E+00	0.999E+00	0.974E+00	0.981E+00	0.987E+00	0.700E+00
4	0.971E+00	0.999E+00	0.992E+00	0.976E+00	0.983E+00	0.450E+00
9	0.229E-01	0.255E+00	0.367E-01	0.566E-01	0.812E-01	0.346E+00
10	0.594E-01	0.194E-01	0.145E-01	0.184E-01	0.265E-02	0.898E+00
11	0.000E+00	0.294E+00	0.884E-01	0.151E-01	0.463E-02	0.768E+00
12	0.294E+00	0.000E+00	0.200E+00	0.294E+00	0.241E+00	0.953E+00
13	0.884E-01	0.200E+00	0.000E+00	0.381E-02	0.501E-02	0.792E+00
14	0.151E-01	0.294E+00	0.381E-02	0.000E+00	0.649E-03	0.970E+00
15	0.463E-02	0.241E+00	0.501E-02	0.649E-03	0.000E+00	0.930E+00
16	0.768E+00	0.953E+00	0.792E+00	0.970E+00	0.930E+00	0.000E+00

Table 22: Proabilities of association of 9 sera, computed by Goodall's (1966) method after removal of data (from Tables 12-14) on sera 2-8. Probabilities are given in E-form.

Sera	Sera 1	9	10	11	12
1	0.000E+00	0.762E+00	0.990E+00	0.978E+00	0.999E+00
9	0.762E+00	0.000E+00	0.161E+00	0.115E+00	0.695E+00
10	0.990E+00	0.161E+00	0.000E+00	0.233E+00	0.103E+00
11	0.978E+00	0.115E+00	0.233E+00	0.000E+00	0.736E+00
12	0.999E+00	0.695E+00	0.103E+00	0.736E+00	0.000E+00
13	0.944E+00	0.111E+00	0.581E-01	0.272E+00	0.503E+00
14	0.998E+00	0.121E+00	0.687E-01	0.441E-01	0.638E+00
15	0.997E+00	0.281E+00	0.259E-01	0.160E-01	0.566E+00
16	0.233E-01	0.307E+00	0.998E+00	0.995E+00	0.999E+00

Sera	13	14	15	16
1	0.944E+00	0.998E+00	0.997E+00	0.233E-01
9	0.111E+00	0.121E+00	0.281E+00	0.307E+00
10	0.581E-01	0.687E-01	0.259E-01	0.998E+00
11	0.272E+00	0.441E-01	0.160E-01	0.995E+00
12	0.503E+00	0.638E+00	0.566E+00	0.999E+00
13	0.000E+00	0.203E-01	0.321E-01	0.984E+00
14	0.203E-01	0.000E+00	0.391E-02	0.999E+00
15	0.321E-01	0.391E-02	0.000E+00	0.999E+00
16	0.984E+00	0.999E+00	0.999E+00	0.000E+00

Table 23: Probabilities of association of 7 sera, computed by Goodall's (1966) method, after removal of data (from Tables 12-14) on sera 2-8 and 14-15. Probabilities are given in E-form.

Sera	Sera						
	1	9	10	11	12	13	16
1	0.000E+00	0.756E+00	0.951E+00	0.932E+00	0.994E+00	0.834E+00	0.249E-01
9	0.756E+00	0.000E+00	0.473E-01	0.103E+00	0.550E+00	0.302E-01	0.460E+00
10	0.951E+00	0.473E-01	0.000E+00	0.862E-01	0.851E-01	0.882E-02	0.992E+00
11	0.932E+00	0.103E+00	0.862E-01	0.000E+00	0.640E+00	0.105E+00	0.985E+00
12	0.994E+00	0.550E+00	0.851E-01	0.640E+00	0.000E+00	0.387E+00	0.999E+00
13	0.834E+00	0.302E-01	0.882E-02	0.105E+00	0.387E+00	0.000E+00	0.946E+00
16	0.249E-01	0.460E+00	0.992E+00	0.985E+00	0.999E+00	0.946E+00	0.000E+00

Table 24: Probabilities of association of 5 sera, computed by Goodall's (1966) method, after removal of data (from Tables 12-14) on sera 2-8, 10 and 13, 14-15. Probabilities are given in E-form.

Sera	Sera				
	1	9	11	12	16
1	0.000E+00	0.745E+00	0.739E+00	0.990E+00	0.199E-01
9	0.745R+00	0.000E+00	0.144E-01	0.965E-01	0.567E+00
11	0.739E+00	0.144E-01	0.000E+00	0.220E+00	0.967E+00
12	0.990E+00	0.965E-01	0.220E+00	0.000E+00	0.998E+00
16	0.199E-01	0.567E+00	0.967E+00	0.998E+00	0.000E+00

Table 25: Probabilities of association between the groups of sera designated, computed by Goodall's (1966) method, using the mean values for each character for all sera in each group. Probabilities are given in E -form. Data from Tables 12-14.

Sera	1	2-4	5-8	9	10+13
1	0.000E+00	0.225E+00	0.299E+00	0.170E+00	0.392E+00
2-4	0.225E+00	0.000E+00	0.381E+00	0.998E+00	0.999E+00
5-8	0.299E+00	0.381E+00	0.000E+00	0.979E+00	0.997E+00
9	0.170E+00	0.998E+00	0.979E+00	0.000E+00	0.261E-02
10+13	0.392E+00	0.999E+00	0.997E+00	0.261E-02	0.000E+00
11	0.335E+00	0.997E+00	0.992E+00	0.213E-01	0.140E-01
12	0.489E+00	0.999E+00	0.999E+00	0.671E-01	0.376E-01
14+15	0.674E+00	0.999E+00	0.996E+00	0.225E-01	0.324E-02
16	0.291E-01	0.765E+00	0.648E+00	0.168E+00	0.571E+00

Sera	11	12	14+15	16
1	0.335E+00	0.489E+00	0.674E+00	0.291E-01
2-4	0.997E+00	0.999E+00	0.999E+00	0.765E+00
5-8	0.992E+00	0.999E+00	0.996E+00	0.648E+00
9	0.213E-01	0.671E-01	0.225E-01	0.168E+00
10+13	0.140E-01	0.376E-01	0.324E-02	0.571E+00
11	0.000E+00	0.924E-01	0.922E-02	0.508E+00
12	0.924E-01	0.000E+00	0.136E+00	0.609E+00
14+15	0.922E-02	0.136E+00	0.000E+00	0.838E+00
16	0.508E+00	0.609E+00	0.838E+00	0.000E+00

Table 26: Probabilities of association between the groups of sera designated, computed by Goodall's (1966) method, using the mean values for each character for all sera in each group. Probabilities are given in E-form.

Sera	Sera 1	2-4	5-8	9-15	16
1	0.000E+00	0.214E+00	0.444E+00	0.127E+00	0.105E-01
2-4	0.214E+00	0.000E+00	0.202E+00	0.994E+00	0.928E+00
5-8	0.444E+00	0.202E+00	0.000E+00	0.978E+00	0.834E+00
9-15	0.127E+00	0.994E+00	0.978E+00	0.000E+00	0.180E+00
16	0.105E-01	0.928E+00	0.834E+00	0.180E+00	0.000E+00

TABLE 27

Percent reactions of Anti-*Chelodina oblonga* with eight tortoise sera, obtained by nephelometric analysis.

Chelodina oblonga	100.0%
Chelodina steindachneri	77.6%
Chelodina expansa	75.8%
Chelodina longicollis	75.4%
Pseudemydura umbrina	59.1%
Elseya latisternum	50.9%
Emydura macquaria	34.5%
Testudo graeca	18.5%

TABLE 28

Distribution of the Australian Chelidae

(see Figure 26)

Group	SW	W	SE		N		New Guinea
			W SE	E SE	NE	NW	
Chelodina longicollis	-	steindach-neri	longicollis	longicollis	novae-guineae	novae-guineae	novae-guineae
Chelodina expansa	-	-	expansa	expansa	rugosa	rugosa	sieben-rocki
Chelodina oblonga	oblonga	-	-	-	-	-	-
Elseya	-	-	-	latisternum	latisternum dentata	dentata	novae-guineae
Emydura	-	-	macquaria	kreffti	kreffti	australis	subglob-osa
Pseudemydura	umbrina	-	-	-	-	-	-

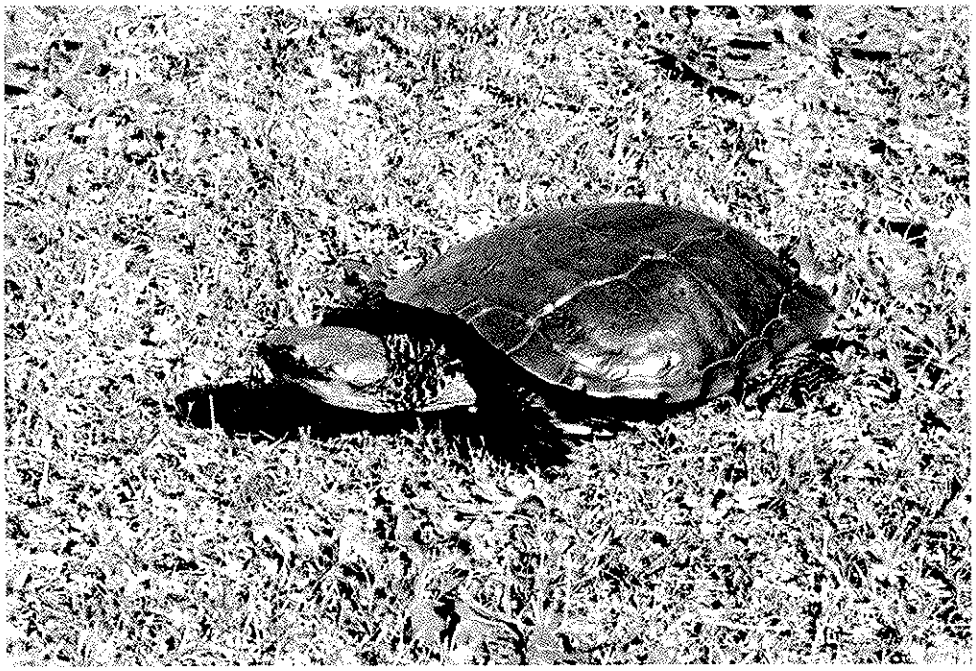


PLATE 1 Pseudemydura umbrina

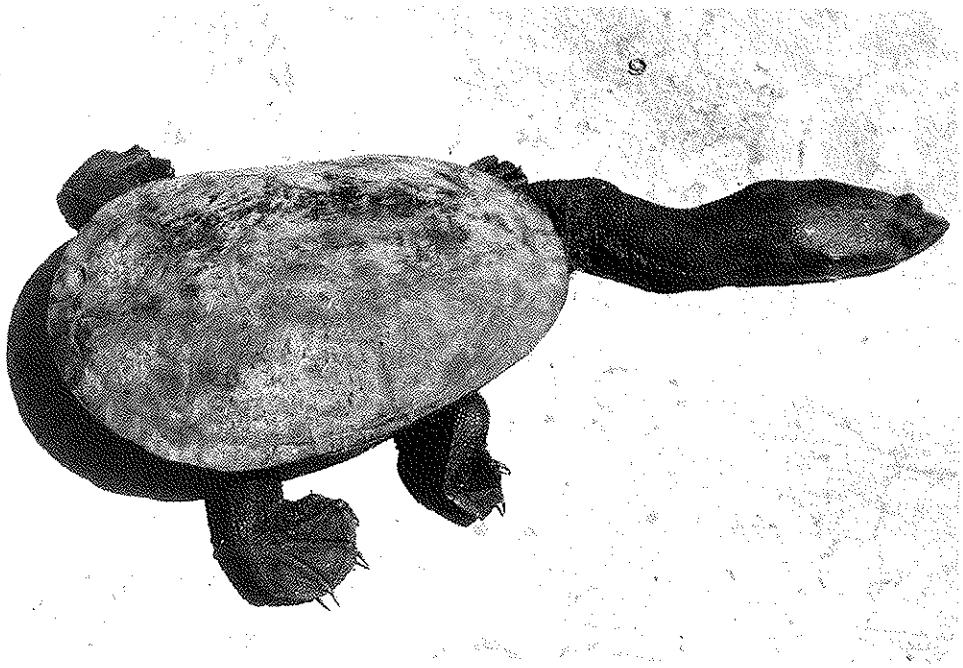


PLATE 2 Chelodina oblonga

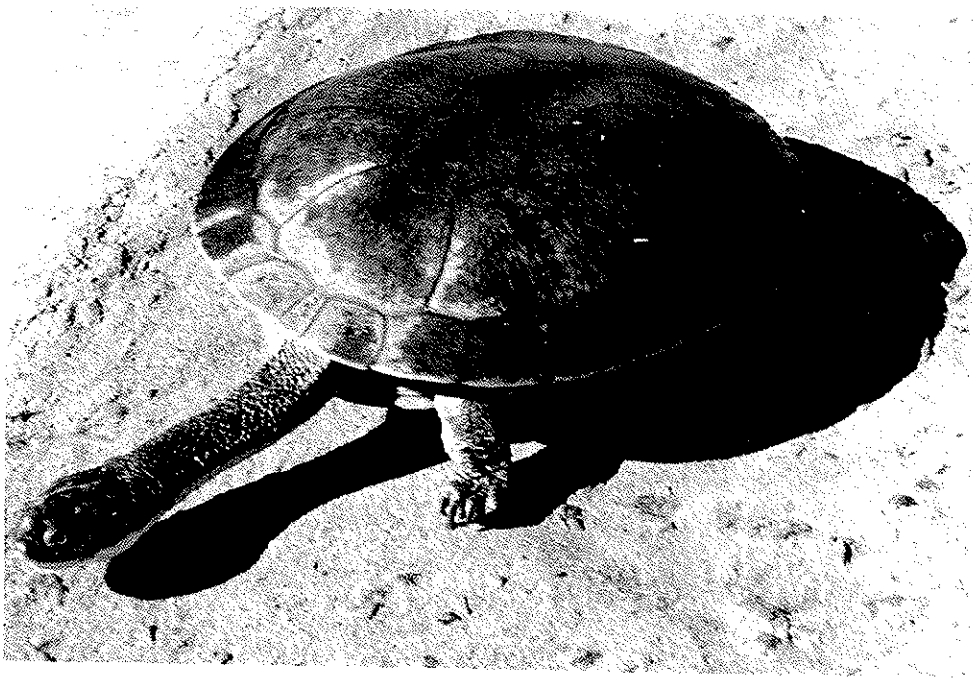


PLATE 3 *Chelodina steindachneri*

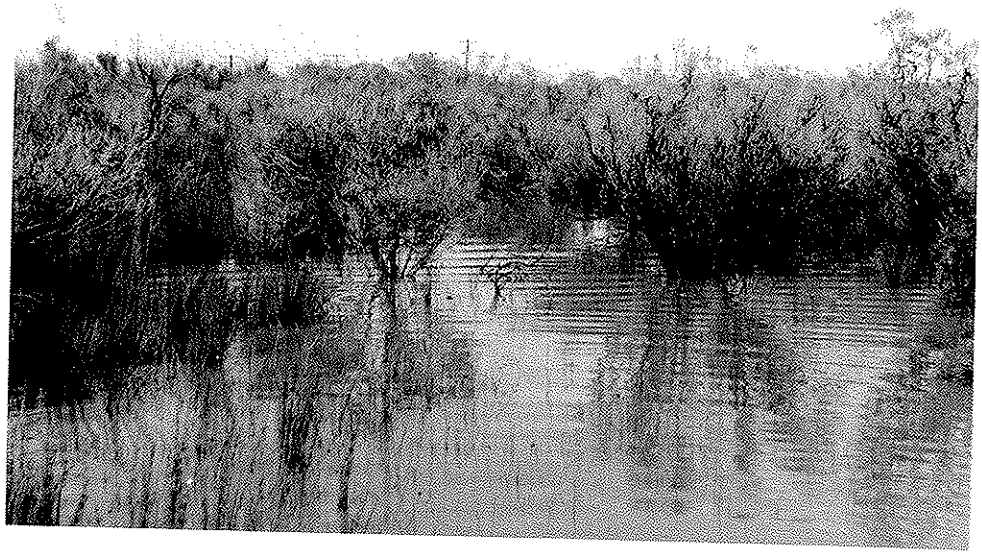


PLATE 4 Ellen Brook Reserve - winter

PLATE 5 Ellen Brook Reserve - summer

PLATE 6 Twin Swamps Reserve
North West Swamp

PLATE 7 Twin Swamps Reserve
East Swamp, dry
Note "feeding depressions"

PLATE 8 Twin Swamps Reserve
South West Swamp

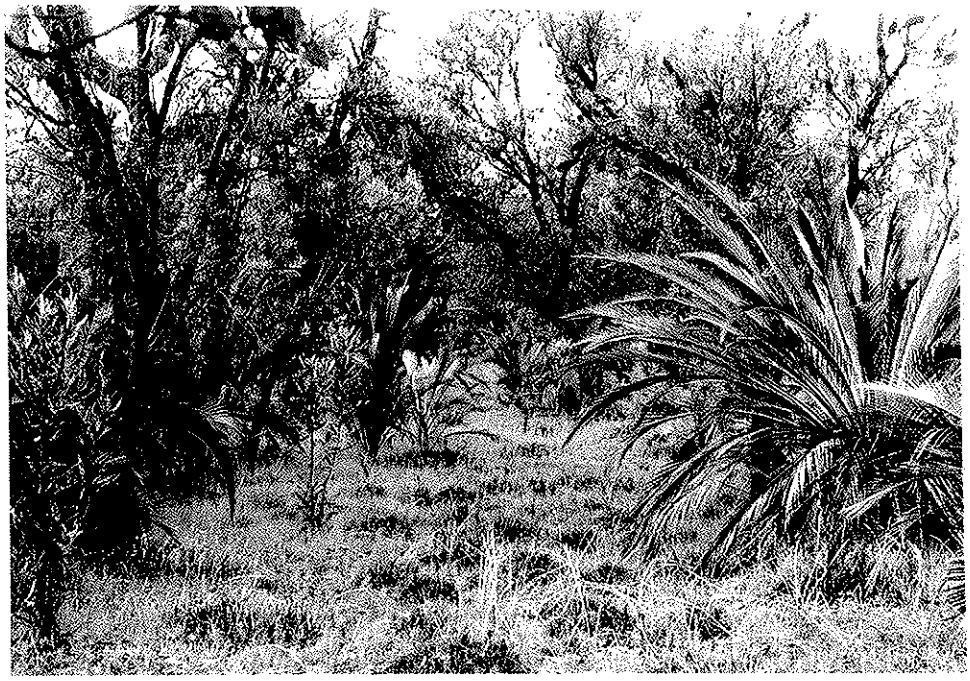


PLATE 9 Twin Swamps Reserve
Banksia woodland

PLATE 10 Twin Swamps Reserve
Regelia association

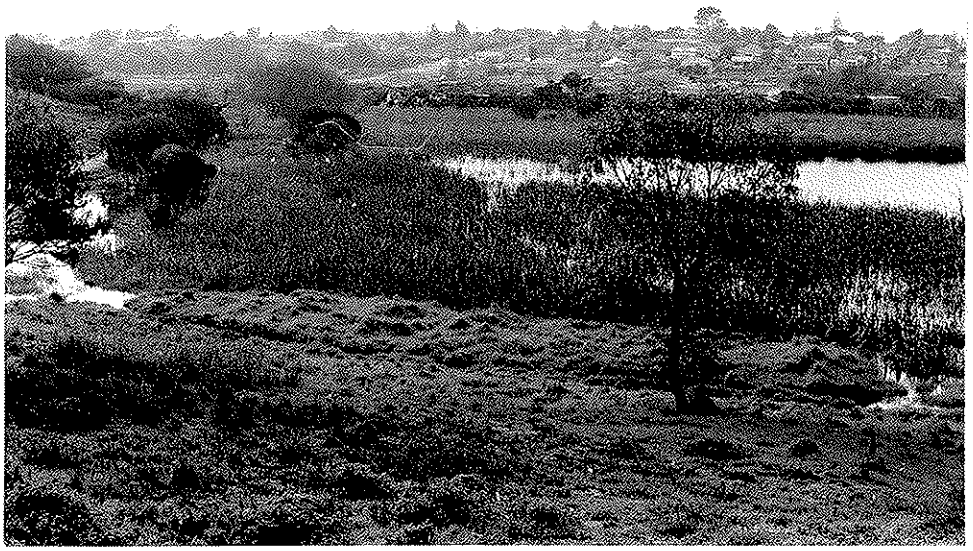


PLATE 11 Lake Claremont
typical *Chelodina oblonga* habitat

PLATE 12 Poonthoon Pool, Mileura Station
typical *Chelodina steindachneri* habitat

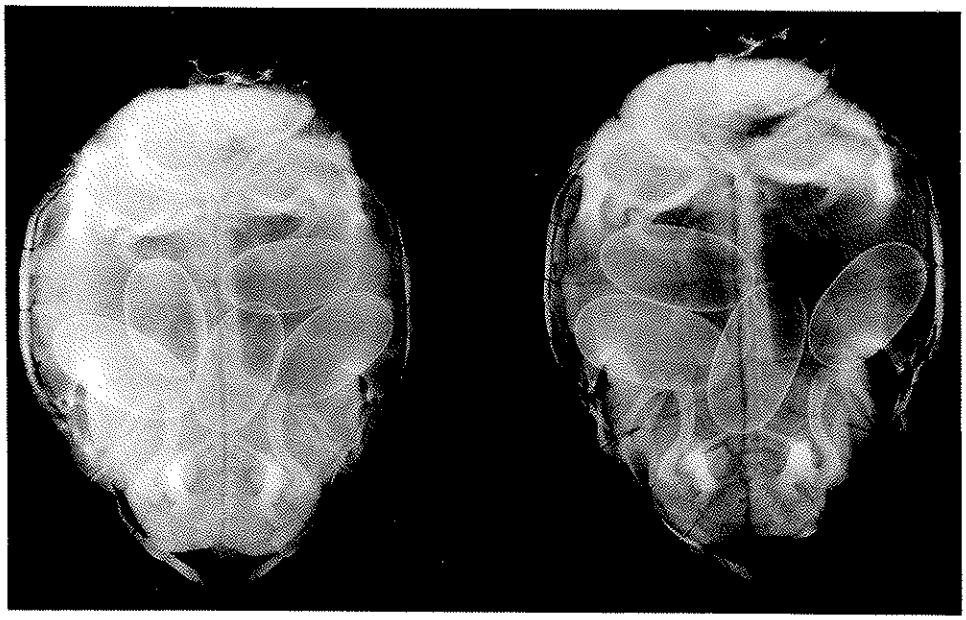


PLATE 13 Radiograph of female P. umbrina
October, 1966

PLATE 14 Twin Swamps Reserve
pit traps around South East Swamp

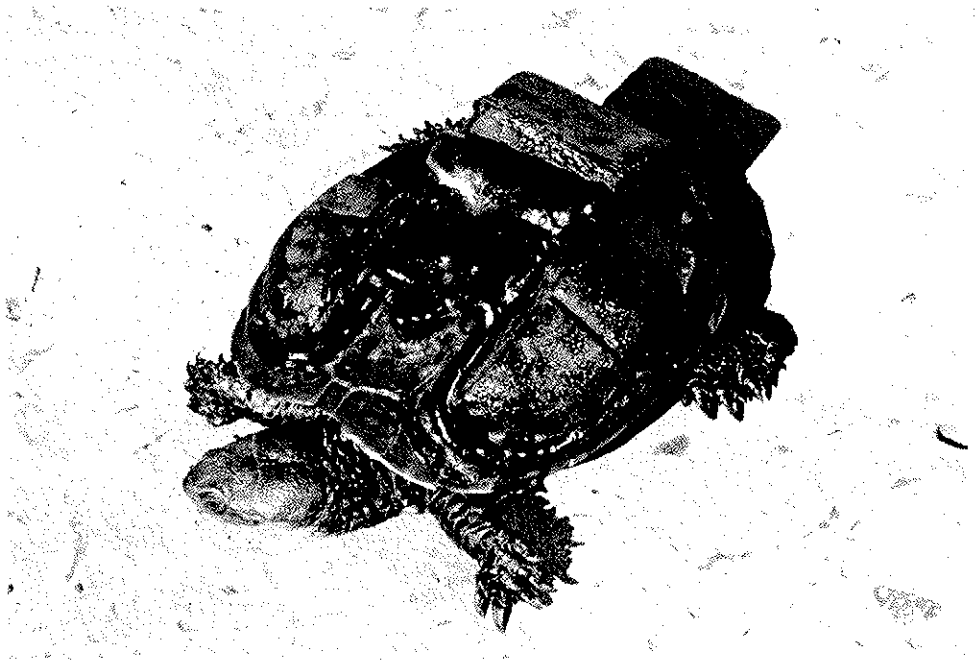


PLATE 15 *Pseudemydura umbrina*
equipped with radio transmitter